

---

# MULTI-SCALE, SOCIAL-ECOLOGICAL INFLUENCES ON PRIVATE LAND CONSERVATION IN SOUTH AFRICA

HAYLEY S. CLEMENTS

---

Supervisor: Professor Graeme Cumming

Co-supervisor: Professor Timm Hoffman

The Percy FitzPatrick Institute

Department of Biological Sciences

University of Cape Town

Thesis presented for the degree of Doctor of Philosophy

November 2016

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.



*“No rounded program for wildlife is possible unless it is applied on private as well as on public lands...”*

*- Aldo Leopold, 1936*

## DECLARATION

I, Hayley Clements, hereby declare that the dissertation for the degree of Doctor of Philosophy is my own work and that it has not previously been submitted for assessment or completion of any postgraduate qualification to another University or for another qualification.

Signature: 

Signed by candidate
---------------------

 Date: 20 November 2016  
Signature Removed

## ABSTRACT

In understanding the behaviour of social-ecological systems, much focus has been placed on the role of institutions that govern how natural resources should be managed, and the biophysical processes affected by this management. Somewhat less attention has been given to the role played by the natural resource managers themselves. Novel insight into social-ecological systems can be gained from understanding why managers act as they do and how management actions become reinforced into (un)sustainable management regimes. In this thesis I applied a social-ecological systems perspective to the phenomenon of private land conservation. With increasing interest in the role that the private sector can play in global conservation efforts, a pertinent but largely unexplored question is whether private land conservation areas (PLCAs) can conserve biodiversity over sufficiently long time scales. This thesis contributes to social-ecological systems theory through an in-depth analysis of the multi-scale interactions among natural resources, managers and socioeconomic processes, which affect PLCA management practices and their sustainability. The potential ability for commercially operated PLCAs to generate the funds necessary for their maintenance makes them an attractive conservation strategy in an economically-orientated world. There are concerns, however, that (a) their long-term sustainability may be dependent on their ability to become and remain financially viable; and (b) they may be tempted to prioritize profit over biodiversity protection in their management practices, thereby jeopardizing their ecological sustainability. The objectives of this thesis were to investigate *if, how* and *why* commercial PLCA managers (a) meet their financial objectives and (b) adopt unsustainable ecological management practices. During 2014 and 2015 I interviewed the managers of 72 commercial PLCAs in the Western and Eastern Cape Provinces of South Africa, a region that supports a rapidly growing yet poorly understood PLCA industry. I applied theories from organizational ecology to understand patterns in the income-generating strategies adopted by PLCA managers. Distinct business models were evident, differentiated by incompatibilities in the biophysical (size, fauna) and socioeconomic (activities, affordability) characteristics of these conservation areas. PLCAs characterized by financial objectives but unprofitable business models suggest that these incompatibilities constrain the ability of managers to effectively adapt to their economic environment, a concept known as “structural inertia” in organizational ecology. Profitability was highest on PLCAs that supported megaherbivores and large predators, reflecting international

tourist preferences for charismatic game. Managers' financial objectives influenced the strategies that they employed to manage these mammals. When managers used revenue-generation to inform their management decisions, they undertook management actions that enabled them to maximize and stabilize game populations. While this intensive management resulted in higher revenues, it corresponded in many cases with a lack of ecological monitoring and an increased risk of overstocking game. Regional policy guidelines for large predator management both mitigated and exacerbated the mismatch between financially-desirable and ecologically-sustainable management, depending on whether species-specific guidelines were ecologically appropriate or not. Simulations of a mechanistic PLCA model were used to test whether adopted management strategies influenced the observed constraints on business model adaptation. If the income-generating potential of an adopted business model was low, managers were unable to accumulate the capital necessary to overcome the biophysical and socioeconomic incompatibilities that separated business models, constraining their adaptive capacity. Intensively managed PLCAs were able to generate a more stable annual income, accumulate more capital and overcome constraints on adaptation faster than PLCAs managed according to ecological monitoring. This unique, large-sample assessment of the social-ecological mechanisms underlying PLCA sustainability emphasizes the significant role that managers can play in promoting resilient social-ecological systems. When financial viability is an important consideration, broad-scale socioeconomic factors can influence fine-scale management decisions. Through constraints on adaptation, and the presence or absence of corrective feedbacks between management actions and ecological monitoring, these management decisions can become reinforced into management regimes on a trajectory towards, or away from, sustainability. This study therefore provides a novel contribution to our understanding of how the interactions between managers and ecosystems influence the behaviour of social-ecological systems.

**Keywords:** action-outcome feedback; natural resource manager; organizational studies; private land conservation; private protected area; profitability; social-ecological system; sustainability

## ACKNOWLEDGEMENTS

I gratefully acknowledge GreenMatter and the Harry Crossley Foundation, the National Research Foundation (NRF) and the German Academic Exchange Service (DAAD), and the University of Cape Town for funding this degree. I am grateful for additional project funding support from the NRF Centre of Excellence at the Percy FitzPatrick Institute and the James S. McDonnell Foundation.

A huge thank you to Graeme Cumming for your guidance over the past three years. I feel immensely privileged to have had the opportunity to work with you. You challenged me to think more broadly, deeply and theoretically, and I feel that I have grown a great deal as a result of your guidance. Thank you for the incredible opportunity to spend a year in Australia. And thank you for your mentorship in my broader career planning as well. I look forward to working with you further!

Thank you very much to Timm Hoffman, I was a bit of a surprise student, and I am grateful to you for agreeing to supervise me so late in the game. I really appreciate your input on my thesis and the paperwork you did for my submission.

Thank you to Graham Kerley for your continued mentorship, for which I am very grateful.

To the Fitz crew – I couldn't have imagined a more positive and friendly place to do my PhD and I thank all the academics, support staff and students for the role they played in creating such a fantastic environment. The Friday pub sessions were a highlight! David, Judith and Andrew, thank you for your good company on my field trips. In particular, thanks to the Cumming lab – Alta, Chevonne, Christine, Dom, Judith, Julia, Kristi and Leo (and Petra as an honorary member!). Thank you for all the stimulating chats, moral support and lunch breaks. You are an incredible, talented group of people. I am grateful to call some of you my good friends. Chev, our many PhD chats, yoga sessions and bottles of wine played a massive role in maintaining my sanity ☺

Thank you to the GreenMatter team and fellows (especially Linda and Eleonore). GreenMatter is so much more than a fellowship; it has been an incredible opportunity to grow professionally and personally and I have gained so much from this wonderful, supportive group. I hope to continue to be an ambassador for South Africa's biodiversity.

A big thank you to the landowners and managers that agreed to participate in this study. I was overwhelmed by your friendliness, openness, hospitality, and your unique pieces of wilderness. The year I spent travelling around the cape, seeing places I have never seen before and learning from you all, is an experience that I will never forget. It reinforced my passion for our beautiful country, its people and its environment. Thank you.

To my family, and particularly my parents, I cannot begin to describe the gratitude I feel. You supported my interest in nature right from the start. I am immensely grateful for the education you gave me, both in and out of school. Our family discussions around the dinner table, for as long as I can remember, have taught me to think carefully and openly. Thank you for supporting me, encouraging me and believing in me.

Alwyn. Thank you for your constant support and encouragement, for putting up with me talking about science way too much, and for all the pep talks and good ideas. Thank you for basically planning our wedding, and then letting me drag you to a different continent, where you got eaten by mosquitos and couldn't go surfing. Life is an adventure with you and I am so grateful to have you in my life.



## TABLE OF CONTENTS

<b>CHAPTER 1:</b> General introduction .....	1
<b>CHAPTER 2:</b> Study region and general methods .....	21
<b>CHAPTER 3:</b> Money and motives: an organizational ecology perspective on private land conservation .....	33
<b>CHAPTER 4:</b> Positives and pathologies of natural resource management on private land conservation areas .....	52
<b>CHAPTER 5:</b> Predators on private land: broad-scale socioeconomic interactions influence large predator management.....	72
<b>CHAPTER 6:</b> Traps and transitions in private land conservation.....	86
<b>CHAPTER 7:</b> Synthesis .....	109
<b>REFERENCES</b> .....	131

## PAPERS ARISING FROM THIS THESIS

The following manuscripts have been published or submitted for review. Published manuscripts have not been included in this thesis verbatim and have been edited and formatted to fit with the rest of the thesis. In all instances, H.S.C. undertook study design, literature review, data collection and analysis, and writing of manuscripts. G.S.C. acted in a supervisory capacity, aiding in study conceptualization and design, and providing valuable feedback on written manuscripts. J.B. provided contact details and additional data for 30 study sites, and provided comments on the written manuscript. G.I.H.K. contributed to study conceptualization, and provided policy information and comments on the written manuscript.

Clements, H. S., J. Baum, and G. S. Cumming. 2016. Money and motives: an organizational ecology perspective on private land conservation. *Biological Conservation* **197**:108–115.  
<http://dx.doi.org/10.1016/j.biocon.2016.03.002>

Clements, H. S., and G. S. Cumming. Positives and pathologies of natural resource management on private land conservation areas. *Conservation Biology*, In press.  
<http://onlinelibrary.wiley.com/doi/10.1111/cobi.12864/full>

Clements, H. S., G. S. Cumming, and G. I. H. Kerley. 2016. Predators on private land: broad-scale socioeconomic interactions influence large predator management. *Ecology and Society* **21**:45. (Special Feature on Private Land Conservation)  
<http://dx.doi.org/10.5751/ES-08607-210245>

Clements, H. S., and G. S. Cumming. Traps and transformations in private land conservation. *Conservation Biology*, In review.

## CHAPTER 1: GENERAL INTRODUCTION

---

Solutions to society's environmental challenges do not fall within the bounds of a single scientific discipline. The overexploitation of natural resources, such as fish stocks and forests, is driven by human population growth, increased access to global markets, financial motivations and technological innovations that improve harvesting efficiency (Berkes et al. 2006; Mora et al. 2011; Cinner et al. 2013; Squires & Vestergaard 2013). Similarly, species and habitat losses result from legal, cultural, financial and political processes, and have significant implications for the provision of ecosystem goods and services, and thereby human well-being (Costanza et al. 1997; Millenium Ecosystem Assessment 2005; Defries et al. 2007; Koontz & Bodine 2008; Coomes et al. 2011). Society's environmental challenges emerge from complex relationships between ecosystems and social (including political and economic) systems (Holling 2001; Berkes et al. 2003; Millenium Ecosystem Assessment 2005; Norgaard 2008). Addressing these challenges necessitates interdisciplinary theories with which to understand complex human-nature interactions.

A social-ecological system can be defined as a set of social and ecological components that interact in a constantly evolving and interdependent manner, with society both depending on and modifying natural resources and the ecosystems that produce them (Berkes et al. 2000; Gunderson & Holling 2002). Social-ecological systems thinking is a new and rapidly growing field of study, aimed at developing and testing theories with which to understand how social-ecological systems function (Daily 1997; Levin 1998; Rockström et al. 2009; Ostrom 2009b; Cumming 2014). Given the young and interdisciplinary nature of this field, many of its ideas and concepts are contested and in need of clarification, and several knowledge gaps remain.

In this thesis I aim to advance social-ecological systems theory by applying a social-ecological perspective to the phenomenon of private land conservation. With interest increasing in the role that the private sector can play in global conservation efforts, a pertinent but largely unexplored question is whether private land conservation areas (PLCAs) can be relied upon to conserve biodiversity into the future. I make the argument that this question cannot be answered by viewing PLCAs simply as ecological systems. Their sustainability is likely to be influenced by their managers' objectives and adopted management strategies, as well as by broader-scale socioeconomic processes such as wildlife policies and tourist markets. This thesis therefore aims

to contribute to social-ecological systems theory through an in-depth analysis of the multi-scale interactions among ecosystems, managers and broad-scale socioeconomic processes, which influence PLCA management practices and their sustainability.

This introduction first outlines the evolution of social-ecological systems thinking and the associated knowledge gaps that this thesis addresses. The challenges encountered by statutory protected areas as society's primary in-situ conservation strategy are then described, and the emerging global phenomenon of private land conservation is assessed as an alternative, complementary strategy. I propose that insight into the sustainability of private land conservation can be gained by adopting a social-ecological systems perspective, and conclude with my thesis objectives and key research questions.

### **1.1 Social-ecological systems theory and current knowledge gaps**

Central to the field of social-ecological systems thinking is the concept that social-ecological systems are complex adaptive systems. Interactions between system components result in emergent properties which cannot be predicted or explained by the individual components (Holland 1995; Levin 1999). These interactions occur over multiple spatial and temporal scales, and can lead to feedbacks that either maintain the system within its current state, or shift it across a threshold and into an alternate state (Levin 1998). Social-ecological systems have the capacity to adapt to their environment through self-organization and learning (Holland 2006). While drawing deeply on complexity theory, social-ecological systems thinking includes central societal concerns, such as human well-being, which receive little attention in complex systems theory (Cumming 2011).

In the 1970's, C.S. Holling challenged the widely-held belief that the natural resource flows from an ecosystem could be controlled and that nature would restore to an equilibrium state if human stressors were removed. He proposed that natural resource systems have multiple stable states or "basins of attraction", and that human actions can erode the ability of a resource system to remain within a state that is desirable to society (Holling 1973). The concept of resilience was introduced and later refined to characterize the following three properties of a complex, adaptive social-ecological system: (a) the amount of change a system can undergo and still remain within the same basin of attraction; (b) the degree to which a system is capable of self-organization; and (c) the degree to which a system can build the capacity to learn and adapt (Holling 1973; Carpenter

et al. 2001). Holling distinguished this “social-ecological system” definition of resilience from the equilibrium-orientated “engineering” definition proposed by S. Pimm in the 1980’s, namely “the ability of a system to resist disturbance and the rate at which it returns to equilibrium following disturbance” (Pimm 1984; Gunderson & Holling 2002). This distinction has led to much debate in the scientific world. The concept of social-ecological resilience was originally criticized due to the lack of empirical evidence for multiple stable states in ecosystems. Despite the substantial body of literature that has emerged since the 1970’s to support the multiple states concept, both mathematically and empirically (Gunderson 2000; Scheffer et al. 2001; Scheffer & Carpenter 2003; Folke et al. 2004; Rockström et al. 2009), critics continue to make the argument that some ecological processes show no evidence of thresholds between alternate states (Donohue et al. 2016). It has been illustrated mathematically, however, that multiple stable states can exist without thresholds in the underlying processes (Petraitis & Hoffman 2010). Furthermore, it can be almost impossible to adequately meet the demands of skeptics for empirical evidence of multiple stable states, given the limited availability of sufficiently large spatial scale data and sufficiently long time-series data (Scheffer & Carpenter 2003). Therefore, while the concept that human and natural systems are intrinsically interlinked is generally accepted, debate continues on the behaviour of these linkages and their outcomes.

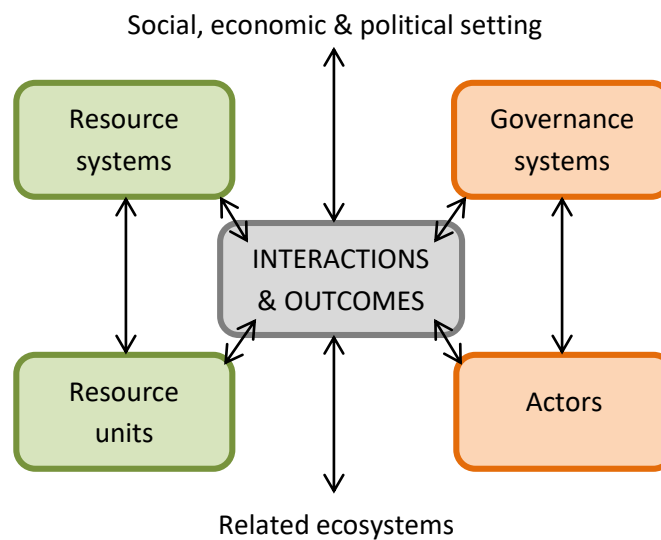
Adopting the social-ecological systems definition of resilience, adaptive capacity refers to the ability of a system to adjust to changing internal demands and external circumstances (Carpenter & Brock 2008). It reflects the capacity of actors in a system to manage resilience, successfully avoiding crossing into an undesirable system state or succeeding in crossing into a desirable one (Walker & Holling 2004). Transformation, in contrast, is the process of creating a fundamentally new system with a new stability landscape, when ecological, economic, or social factors make the existing system untenable (Walker & Holling 2004; Walker et al. 2006). Transformation to a fundamentally new system can, however, prove difficult to distinguish from adaptation within an existing system, and sometimes systems display resilience in the absence of adaptation and learning (Walker & Holling 2004; Walker et al. 2006; Moore et al. 2015). Vulnerability refers to the degree to which a system, subsystem, or system component is likely to experience harm due to exposure to a perturbation or stress, through an inability to either adapt or transform (Turner et al. 2003). While vulnerability research traditionally focused on social systems and did not consider the vulnerability of biophysical systems, more recent approaches

acknowledge that human and biophysical vulnerabilities are linked and should be treated as such (Turner et al. 2003; Adger 2006; Gallopin 2006; Smit & Wandel 2006). Distinguishing quantitatively between different outcomes in an analysis of a system's response to a stress or disturbance therefore requires a clear definition of the system of interest and the measurement of relevant, analytically tractable variables that can capture changes in the system properties of interest (Moore et al. 2015).

The ability to develop, test, clarify and extend the theoretical underpinnings of social-ecological systems is dependent on effective frameworks with which to integrate an ever-increasing number of findings, emerging from a range of disciplines that differ in their focus, epistemologies, theories and tools (Cumming 2014; Cox et al. 2016). For example, sustainability science focusses on sustainable development and the need to reconcile society's development goals with the planet's environmental limits over long time scales (Kates et al. 2001; Clark et al. 2003). Inspired by thermodynamics (flows of energy and matter), systems thinking, and a need to address the lack of consideration of ecological limits to growth in neoclassical economics, ecological economists emphasize that the human economy is embedded in nature (Costanza 1989; Ropke 2004). Adaptive management seeks to explain how social and natural systems learn through experimentation (Walters 1986; Allen & Gunderson 2011), and political ecology emphasizes the complex interrelations between local people, national and global political economies, and ecosystems (Wolf 1972; Blaikie & Brookfield 1987).

Numerous social-ecological systems frameworks have been developed in an attempt to integrate the social-ecological systems literature into a coherent body of theory, including Panarchy, the Resilience Alliance workbook and the sustainability framework (see review by Cumming 2014). The sustainability framework developed by E. Ostrom is a widely used theory-oriented framework, which attempts to define and connect different pieces of theory within social-ecological systems research (Ostrom 2007, 2009b). It presents a standard framework for classifying a social-ecological system into its components and relationships (Fig. 1; Ostrom 2009b). The four core components are the resource system (such as a coral reef), the resource units (such as fish populations occurring on the reef), the actors (such as fishers), and the governance system (such as institutions and organizations that regulate the fishery). Social-ecological system behaviours, such as self-organization and adaptation, are believed to emerge from multidirectional

interactions between the system components and their outcomes, as well as from linkages across levels of governance, or between ecosystems (Fig. 1).



**Fig. 1.** A simplified version of the sustainability framework for analyzing social-ecological systems (Ostrom 2009b). Ecological and social system components are represented in green and orange, respectively.

The last 25 years have seen substantial changes in perspectives on governance, which support the theory that social-ecological systems emerge from self-organizing system components. The notion of government as the sole decision-making authority has been replaced by multi-scale, polycentric governance perspectives that recognize the contribution of a large number of system agents, functioning across diverse institutional settings (Ostrom 1990, 2010; Folke et al. 2005). Recognition of the importance of institutions for governing social-ecological systems is widespread (Ostrom 1990, 2009a; Barrett et al. 2001; Brunckhorst 2002; Anderies et al. 2004; Hilborn et al. 2005; Hayes 2006). Institutions are defined as “the humanly derived constraints that shape human interaction” (North 1990), such as laws, rules and traditions. In his seminal paper, *The tragedy of the commons*, Hardin (1968) claimed that without an institutional arrangement of either private property or centralized government, the benefits to individual resource users of overexploitation would result in the collapse of common pool resources. As he predicted, collapses emerged in many unregulated natural resource systems around the world; fisheries are a notable example (Hilborn et al. 2003). More recently, however, it has been shown that self-governing institutions developed by the resource users themselves can facilitate sustainable natural resource management, even in common-pool resource systems (Ostrom 1990). Although these institutions

have not always succeeded, there are many examples where Hardin's preferred institutional alternatives of centralized government or private land ownership have failed (Dietz et al. 2003).

Somewhat less attention in social-ecological system analysis has been paid to the role of organizations, despite their importance in ecosystem governance (Clarke & McCool 1996). The international network of protected areas, for example, is one of the conservation community's most important means of safeguarding biodiversity, yet underfunding and competing priorities jeopardize the ability of government organizations to effectively govern existing protected areas (Bruner et al. 2004). These challenges are not institutional, since legal frameworks and enforcement measures for the protection of nature exist; they are primarily organizational. Within conservation science, there has been recent interest in assessing the likely long-term effectiveness of conservation organizations. The ability of managers to adapt their organizations to change, to align their objectives, and to collaborate are believed to be key determinants of organizational effectiveness (Bode et al. 2011; Baral 2013; Gordon et al. 2013; Larson et al. 2014; Armsworth et al. 2015; Guerrero et al. 2015; Iacona et al. 2016; Ruseva et al. 2016). The existing body of theory in the organizational sciences relating to drivers of organizational emergence, adaptation, diversification, success and failure (e.g. Hannan & Freeman 1977; Williamson 1981; Mellahi & Wilkinson 2004; Sydow et al. 2009; Heine & Rindfleisch 2013) has, however, been largely ignored in social-ecological systems research.

There is a substantial body of literature on how actors in natural resource systems (such as resource users or managers) influence the resource units and systems being exploited (Wright & Heinselman 1973; Ludwig et al. 1978; Walker et al. 1981; Anderies et al. 2002). For example, fishing practices influence fish population dynamics, agricultural practices influence water quality in lakes, rangeland management influences vegetation composition, and dams influence flooding regimes (Larkin 1977; Pamo 1998; Carpenter et al. 1999, 2015; Anderies et al. 2002; Folke et al. 2004; Seymour et al. 2010). In each of these cases, there is a recognized trade-off between managing to maximize short-term benefits (often labeled as an 'optimization', 'Maximum Sustainable Yield', or 'Command and Control' approach) and managing for longer-term resilience (Walker et al. 1981; Holling & Meffe 1996; Anderies et al. 2007; Carpenter et al. 2015). For example, the management of fisheries under a maximum sustainable yield paradigm stabilized fish harvests in the short-term, but ultimately resulted in the successive collapses of several globally important fish stocks (Larkin 1977). Other examples where reducing natural ecological variability



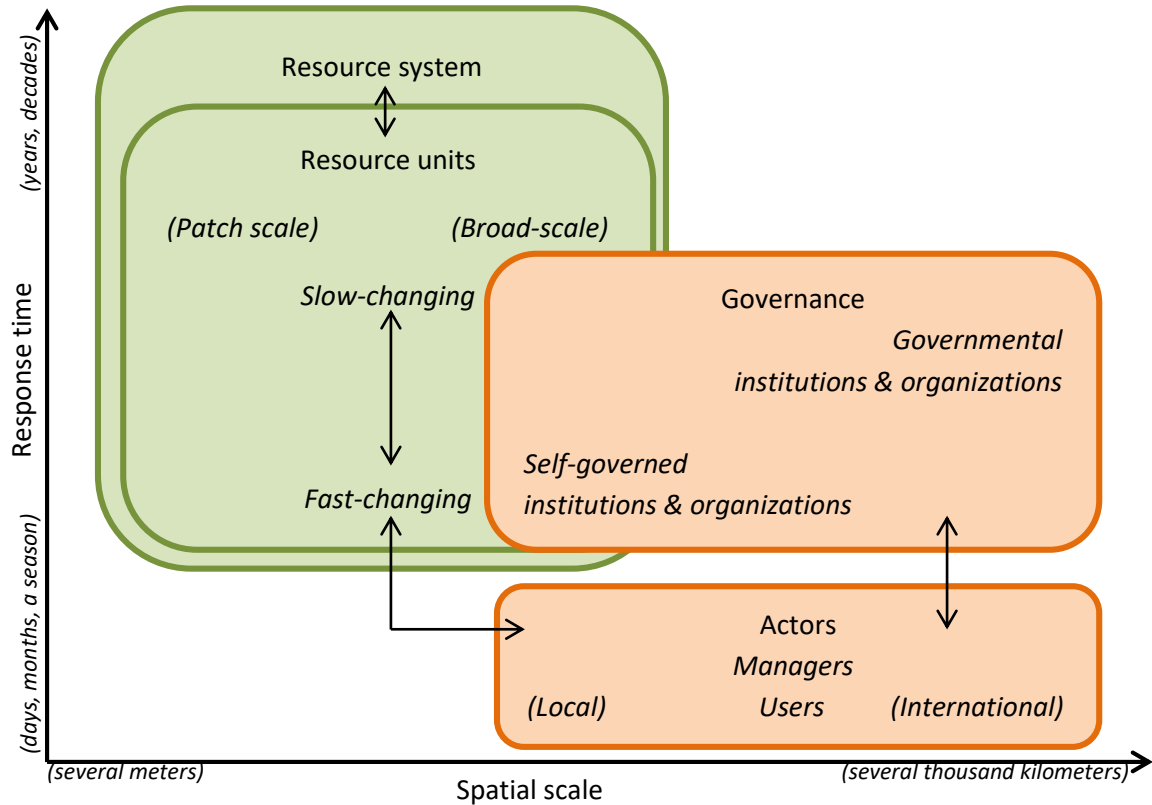
in a resource system for short-term resource optimization has ultimately resulted in disastrous ecological changes include pest control in farming, fire suppression in rangelands and forests, alterations to river flow regimes and the migratory movements of large herbivores, and predator control (Wright & Heinselman 1973; Ludwig et al. 1978; Holling & Meffe 1996; Pamo 1998; Cochrane & Laurance 2002; Allison & Hobbs 2004; Folke et al. 2004). These practices are sufficiently widespread that they have been termed “the pathology of natural resource management” (Holling & Meffe 1996).

Given these challenges, much emphasis has been placed on developing tools to promote effective natural resource management in the face of uncertainty through, for example, adaptive management, learning, decision-theory, robust control frameworks and scenarios (Holling 1978; Walters 1986; Walters & Holling 1990; Carpenter & Gunderson 2001; Anderies et al. 2007; Keith et al. 2011; Polasky et al. 2011; Williams 2015). The motives, social norms and conservation ethics that influence a manager’s decision-making have also attracted considerable attention, particularly in research on farming systems (Beedell & Rehman 1999; Willock et al. 1999a, 1999b; Darnhofer et al. 2005; Janssen & van Ittersum 2007; de Snoo et al. 2013; Poppenborg & Koellner 2013). Management decision-making approaches are likely to be *dynamic*, and emerge from *feedbacks* between managers’ objectives, their management actions, and the outcomes of these actions (Walker & Janssen 2002; Peterson et al. 2003; Anderies et al. 2007; Lindkvist & Norberg 2014). If managers are focused on optimizing yield in a natural resource system, for example, they are likely to respond to observed successes with further command-and-control management, without realizing that these actions gradually reduce the resilience of the managed system until undesirable surprises emerge (Holling & Meffe 1996). This dynamic nature of manager decision-making has been emphasized in several conceptual and modelling papers (Clark 1976; Anderies et al. 2007; Anderies 2015; Carpenter et al. 2015), but empirical evidence is lacking. Furthermore, research in behavioural economics, psychology, and behavioural decision theory suggests that people, including managers, are subject to a range of biases in their perceptions and judgments, which may influence how they perceive and respond to the outcomes of their management actions (Iftekhar & Pannell 2015). Therefore, while there is a substantial body of research on (a) natural resource manager motives and how these influence management, (b) the impact of management on resource units and systems, and (c) proposed tools for managing natural resources in the face of uncertainty,

empirical analyses of the *feedbacks* between manager motives, actions and outcomes are not currently well integrated within social-ecological system research.

The consequences of feedbacks for social-ecological systems behaviour can prove particularly difficult to understand when they involve system components that span multiple scales (McGinnis 2010; Epstein et al. 2013; Creswell et al. 2014; Cumming et al. 2015). Many ecological systems include components that span multiple spatial scales, ranging from localized patches to regional habitats and wide-ranging migratory species (Fig. 2; Poiani et al. 2000). Effective conservation therefore requires the maintenance of key ecosystem functions and processes at multiple spatial scales (Loucks et al. 2004). Similarly, the social system can include components at multiple institutional levels, ranging from local actors and organizations to regional and national laws and international markets (Fig. 2; Cumming et al. 2015). Temporal scales are also important in social-ecological interactions. Faster-changing variables in a system interact with slower-changing variables (Fig. 2; Gunderson & Holling 2002; Norberg & Cumming 2008). For example, agricultural fertilizers influence the slower-changing phosphorous concentration in lake sediments, which determines whether the lake is in a desirable clear-water state or a turbid water state (Carpenter et al. 1999). The outcome of an interaction may therefore not be evident immediately, due to time-lags between the interaction and the appearance of social or ecological outcomes (Liu et al. 2007). Increased nutrient loadings in a lake system can take years to affect water quality, for example (Carpenter et al. 1999).

Many of the challenges encountered by societies in managing natural resource systems arise because of a mismatch between the scale of management and the scale of ecological processes being managed (Cash & Moser 2000; Cumming et al. 2006). In the absence of regional and global governance structures with the power to regulate fishing harvests at spatial and temporal scales appropriate for fish population dynamics, for example, societies have overexploited fish populations (Hilborn et al. 2005). Similarly, the size limitations of fenced protected areas impede natural large-scale movements of elephant *Loxodonta africana*, with the associated increases in elephant densities impacting negatively on other biodiversity within these areas (Kerley & Landman 2006). The effectiveness of conservation actions can be impeded if scale mismatches exist between the time-scales of funding and ecological processes, or the rates of monitoring, action and ecological change (Guerrero et al. 2013).



**Fig. 2.** Conceptual representation of a social-ecological system in space and time. Ecological and social system components are represented in green and orange, respectively. Spatial scale represents the scale at which system components function (from localized species occurring within patches of several meters to migratory species traversing thousands of kilometers; from local organizations making decisions that affect an area of several thousand hectares to governments making nationally-relevant decisions; and from users that live within a few kilometers of a resource system to those that live several thousand kilometers away). Response time represents the time taken for system units to respond to internal or external changes (from species abundances that change over a season to vegetation quality which can take decades to change; and from local organizations which can respond to emergent issues within several months, to national governments which may take several years or decades to respond). As this is a conceptual illustration, box sizes and locations are intended to depict relative scales at which system units may operate, as opposed to providing precise estimates.

In summary, the processes that lead to the conservation or degradation of natural resources arise from complex interactions between governance systems (institutions and organizations), actors (including managers and users), natural resources and natural resource systems. These social-ecological interactions often span multiple spatial and temporal scales (Fig. 2). Since its recent conception, social-ecological systems research has developed into a substantial field of study. Gaps remain, however, in our ability to understand and predict social-ecological system

behaviour. While much focus is placed on the behaviour of institutions and natural resources in social-ecological systems research, managers and their organizations are often viewed as static entities, or overlooked altogether. In this thesis I emphasize that social-ecological systems theory could benefit from improved integration of manager decision-making feedbacks, and concepts from the organizational sciences.

## **1.2 Protected areas and private land conservation areas**

### *1.2.1 Protected areas and private land conservation areas as social-ecological systems*

Given the continued environmental challenges faced by society, including the dramatic human-induced global decline in biodiversity and the habitats on which it depends (Butchart et al. 2010; Barnosky et al. 2011), efforts to curb land-use change and biodiversity loss are increasingly important. Protected areas are recognized as a core strategy for in-situ biodiversity conservation (Bruner et al. 2001; Chape et al. 2005; Geldmann et al. 2013; Edgar et al. 2014). In recognition of their importance, the Convention on Biological Diversity (CBD) Aichi Target 11 outlines ambitious protected area targets of at least 17% of terrestrial and inland water areas and 10% of coastal and marine areas protected by 2020 (CBD 2011). The global protected area estate has grown rapidly over the past century, with national (statutory) protected areas covering 12.5% of Earth's land area (Watson et al. 2014).

Historically, protected areas were established and managed for the preservation of biodiversity through “protectionist” approaches; they were largely state-owned, had no-take (i.e. no resource use) policies and provided little access or direct benefits to society (Naughton-Treves et al. 2005). There is increasing recognition, however, that protected areas do not function in isolation. Their ability to conserve biodiversity is influenced by their context, and their long-term effectiveness is likely to be dependent on their ability to remain relevant to society (Watson et al. 2014; Cumming et al. 2015; Cumming 2016a). Anthropogenic activities around a protected area can influence conservation efforts within the protected area, as many ecosystem functions occur at a scale larger than that which is protected (Hansen & Defries 2007). Statutory protected areas are usually located in the least productive portions of the landscape where the opportunity costs incurred by society are lowest (Norton 2000; Scott et al. 2001; Rouget et al. 2003; Jenkins & Joppa 2009; Devillers et al. 2015; Pressey et al. 2015). There are significant shortfalls in protected area effectiveness globally (Leverington et al. 2010; Laurance et al. 2012), with under-resourced

management recognized as a primary challenge, particularly in developing countries (Bruner et al. 2001). Political pressures on protected areas arise from issues of justice and equity (Adams & Hutton 2007; Spierenburg et al. 2008). Protected areas are therefore social-ecological systems, responding to and influencing a wide range of ecological, social, economic and political processes (Berkes et al. 2003; Strickland-Munro et al. 2010; Ban et al. 2013; Palomo et al. 2014; Cumming et al. 2015).

Given the social and ecological challenges experienced by statutory protected areas, this global network is unlikely to be adequate for effective biodiversity conservation on its own (Leverington et al. 2010; Laurance et al. 2012). Governments, nongovernmental organizations and scientists alike are therefore exploring alternative, complementary strategies for conserving biodiversity. Private land conservation represents one such option (Stolton et al. 2014; Kamal & Brown 2015). Recognizing the potential for private land to contribute to conservation efforts, governments from 154 nations approved a Private Protected Area Action Plan at the World Parks Congress in 2003. The plan was intended “to build a shared understanding of, and vision for, privately owned protected area contributions to international conservation and development and to expand our understanding of protected areas owned by private landowners” (Langholz & Krug 2004). Despite the acknowledgement of private land as an important conservation tool, the lack of a common definition on what constitutes a “private protected area”, and concerns over the likely permanence of this land use, have resulted in private land being omitted from international conservation reporting mechanisms, ignored by governments and excluded from regional conservation strategies (Stolton et al. 2014).

The limited data that are available suggest that the global network of private land conservation areas (PLCAs) is substantial and growing, particularly in some parts of Latin America, including Brazil, Colombia, Chile and Costa Rica; Australia; Canada, the United States of America and Mexico; western and northern Europe; and southern and eastern Africa (Langholz & Lassoie 2001; Stolton et al. 2014; Fitzsimons 2015; Owley & Rissman 2016; Pegas & Castley 2016). Proposed factors driving the emergence of this phenomenon include (a) the public sector’s unwillingness or inability to meet society’s demands for nature conservation; (b) the rising societal interest in biodiversity conservation; and, specific to commercially operated PLCAs, (c) the growth of a global nature-based tourism industry, wildlife-based photo tourism industry and recreational hunting industry (Carter et al. 2008). PLCAs around the world have been shown to

complement conservation on statutory protected areas by conserving sensitive, high-productivity landscapes and riparian areas, improving ecological connectivity between protected areas, and buffering statutory protected areas (Langholz 1996; Swift et al. 2004; Fitzsimons & Wescott 2008; Wallace et al. 2008; Gallo et al. 2009; Lindsey et al. 2014; Pegas & Castley 2016).

PLCA owners include individuals with personal funds, nonprofit organizations supported by the public, for-profit companies managing nature-based tourism operations, and companies that own and manage important wildlife refuges as an offshoot of their operations (see review by Stolton et al. 2014). Some PLCAs are open to the public for free or at a price, while others are for the sole use of their owners (Stolton et al. 2014). The motivations behind PLCA establishment are therefore diverse, ranging from lifestyle preferences, philanthropy and desires to conserve nature, to personal prestige and profit-generation (Langholz 1996; Langholz et al. 2000; Mir & Dick 2012; Stolton et al. 2014; Selinske et al. 2015). Unlike legally-recognized statutory protected areas, PLCAs are often informally protected and their status is thus tenuous (Langholz & Lassoie 2001; Swift et al. 2004). Their diversity in tenure arrangements raises complex issues of ownership, governance and legitimacy (Adams & Hutton 2007; Eagles 2009). In many countries PLCAs are much smaller than statutory protected areas, which makes them vulnerable to edge effects and risks of wildlife overstocking (Langholz 1996; Swift et al. 2004; Cousins et al. 2008; Fitzsimons & Wescott 2008; Child et al. 2013; Spear et al. 2013; Pegas & Castley 2014, 2016). Management has been highlighted as a key determinant of success by PLCA owners (Langholz 1996), with management strategies varying widely across PLCAs (Child et al. 2013). Little is known about the scale and scope of PLCAs globally, their probability of persisting into the future, and thereby the extent and duration of the conservation security that they provide (Carter et al. 2008; Pasquini et al. 2010a; Stolton et al. 2014).

The industry of commercial PLCAs is a particularly interesting phenomenon, which is growing in many parts of the world (Langholz 1996; Swift et al. 2004; Sims-Castley et al. 2005; Castley 2010; Pegas & Castley 2014; Stolton et al. 2014). While the potential ability of PLCAs to generate the funds necessary for their maintenance makes them an attractive conservation strategy in an economically-orientated world (Langholz & Krug 2004), there are concerns that (a) their long-term sustainability may be dependent on their ability to become and remain financially viable; and (b) they may be tempted to prioritize profit over biodiversity protection in their management practices, thereby jeopardizing their ecological sustainability (Langholz 1996; Isaacs 2000;

Langholz & Lassoie 2001; Sims-Castley et al. 2005; Cousins et al. 2010; Pasquini et al. 2010b; Miller et al. 2013; Maciejewski & Kerley 2014a). For example, many commercial PLCAs in South Africa stock extralimital species (i.e. species occurring outside their historic range) such as giraffe *Giraffa camelopardalis* in the Eastern Cape, or stock charismatic large mammals at high densities, for ecotourism or hunting purposes (Cousins et al. 2010; Child et al. 2013; Maciejewski & Kerley 2014a, 2014b). These actions can have negative effects on vegetation, as well as invertebrate, bird and mammal communities (Castley et al. 2001; Kerley & Landman 2006). Policies can aid in promoting biodiversity conservation and sustainable management on private land, provided that they are well-aligned with landowner motivations, well-informed, and enforced (Fischer & Bliss 2008; Paloniemi & Tikka 2008; Cousins et al. 2010; Moon & Cocklin 2011; Kusmanoff et al. 2016)

Both financial viability and ecological management have the potential to influence the sustainability of commercial PLCAs. Insight into the sustainability of the commercial PLCA industry can therefore be gained through consideration of the social-ecological interactions that influence PLCA management and profitability. This thesis focusses on commercial PLCAs in a region that has seen substantial growth in this industry over the past 20 years but remains poorly understood; the Western and Eastern Cape Provinces of South Africa.

### 1.2.2 *The evolution of commercial private land conservation areas in southern Africa*

The development of improved means of hunting (guns) and transportation (railways) during the industrial revolution enabled hunters to (a) harvest wildlife more productively and efficiently and (b) reach new local and global markets (Child et al. 2012). Without institutions to control the industry, wildlife was decimated in many industrialized countries and their colonies. In southern Africa, epidemics of bovine pleuropneumonia and rinderpest at the turn of the 19th century led to further depletion of wildlife, as well as herds of domestic stock (Child 2004). The response to this perceived extirpation of wildlife in the British colonies of southern Africa was to nationalize wildlife, with the development of three policy decisions that had long-lasting implications (Bond et al. 2004; Child 2004; Child et al. 2012). Firstly, state-owned protected areas were formed (including many of today's national parks), with fences to separate wild and domestic ungulates. Secondly, the subsistence and commercial use of wildlife was restricted, making wildlife valueless. Thirdly, ownership of wildlife was centralized to the state. Commercial and

communal farmers were thereby alienated from wildlife, with little incentive for private landowners to protect wildlife and the responsibility for wildlife conservation resting solely on the state. Wildlife numbers declined significantly outside of protected areas (Child et al. 2012).

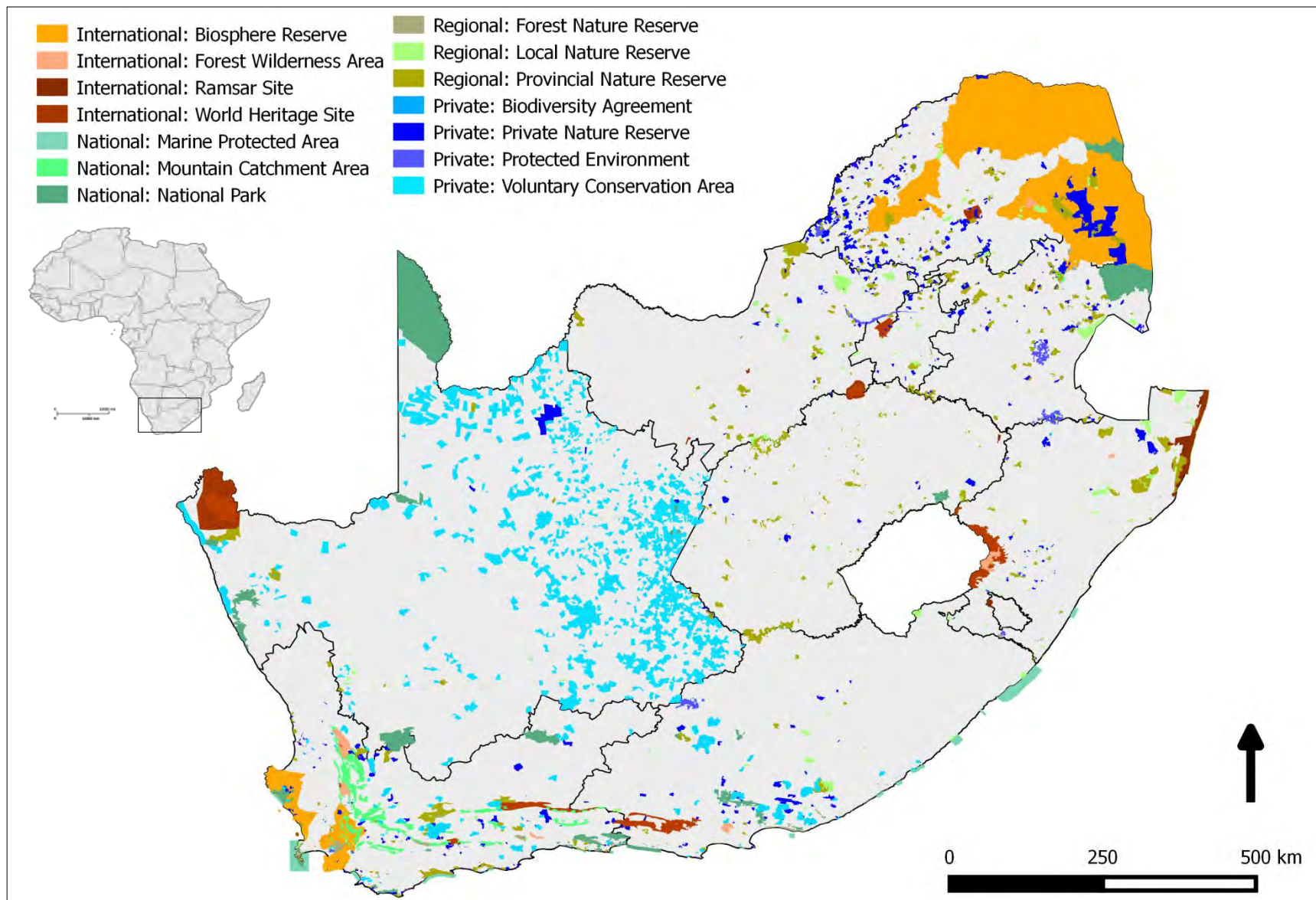
The end of colonial rule in East Africa saw increasing centralization in the control of wildlife, but legislation began emerging in the late 1960's in southern Africa that allowed landowners to use their wildlife commercially (Bond et al. 2004; Child et al. 2012). With these legislative changes, in addition to decreasing profitability of livestock farming and increasing stock theft (Cousins et al. 2008), commercial PLCAs emerged as a new land use in the region. PLCAs proliferated in South Africa, Namibia and Zimbabwe (then Rhodesia), where legislation was most conducive, occurring on a smaller scale in Botswana and Zambia (Bond et al. 2004; Cousins et al. 2008).

These land use changes in the private sector have been largely market driven, with landowners receiving little or no support from the state, either technical or financial (Bond et al. 2004). Wildlife trophy hunting has been the market entry point for many PLCAs (Bond et al. 2004). Non-consumptive wildlife use, in the form of ecotourism, requires a destination with exotic or photographic appeal and entails much higher levels of capital investment (Bond et al. 2004; Novelli et al. 2006). High-end, low-volume ecotourism on private land is nonetheless developing into a significant industry within southern Africa, targeting international tourists from high income countries (Bond et al. 2004; Sims-Castley et al. 2005; Magole & Magole 2011). South Africa also supports a domestic tourism market with demand for lower-end ecotourism and hunting opportunities (Krug 2001; Bond et al. 2004; De Vos et al. 2015). Not all commercial PLCAs in South Africa support large herbivores, with some offering "outdoor" or "scenery" orientated ecotourism opportunities (Baum 2016). Private landowners across the region have proved innovative in their provision of activities and products to meet a diverse market (Krug 2001; Bond et al. 2004; Sims-Castley et al. 2005; Child et al. 2013). By the turn of the century, nature-based tourism was contributing about as much to the gross domestic product of southern Africa as agriculture, forestry and fisheries combined (Scholes & Biggs 2004).

While many commercial PLCAs in South Africa rate profit generation as an important objective, others rate it as unimportant, with conservation values and place attachment stated as the primary drivers behind PLCA establishment (Langholz 1996; Pasquini et al. 2010b; Selinske et al. 2015). The motivations driving this industry are therefore diverse.



Over the past 25 years, growth in the conservation estate in southern Africa has taken place to a large extent outside of statutory protected areas on private land (Krug 2001). With 79% of South Africa's land area privately owned (Department of Rural Development and Land Reform 2013), private land has become an important part of the national conservation effort (Bond et al. 2004). Figure 3 illustrates the diverse institutional bodies responsible for land conservation in South Africa.



**Fig. 3.** The different institutional bodies governing conservation areas in South Africa (De Vos unpubl. data).

### 1.2.3 *A short note on private land conservation terminology*

The International Union for the Conservation of Nature (IUCN) defines a protected area as “a clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (Stolton et al. 2014). A private protected area is defined as “a protected area, as defined by IUCN, under private governance i.e. individuals and groups of individuals; non-governmental organizations (NGOs); corporations; for-profit individuals; research entities (e.g. universities, field stations) or religious entities (Stolton et al. 2014). Many definitions of a private protected area exist, however, and terminology is not applied uniformly (Carter et al. 2008; Stolton et al. 2014; Fitzsimons 2015). For example, Namibian legislation provides for Private Game Reserves and Private Nature Reserves but does not define these entities; many private land holdings are called ‘private game reserve’ or something similar (Stolton et al. 2014). In contrast, in neighbouring South Africa, “Private Nature Reserves” and “Protected Environments” are legally gazetted under the Protected Areas Act, “Biodiversity Agreements” are formal agreements under contract law, and “Conservation Areas” are informal, non-contractual agreements, but receive some form of protection by the landowners and are managed at least partly for biodiversity conservation (Fig. 3; Cadman 2010). Given these differences in terminology, I do not use the term “private protected area” but rather use the more general terms “private land conservation” and “private land conservation area”. This terminology is increasingly used in the research literature (Wallace et al. 2008; Von Hase et al. 2010; Kamal & Brown 2015; Selinske et al. 2015). In this thesis I define private land conservation areas (PLCAs) as “land parcels of any size that are managed for biodiversity conservation and potentially for nature tourism and/or wildlife-based ventures; protected with or without formal government recognition; and owned or otherwise secured by individuals, communities, corporations or nongovernment organizations”.

The PLCAs in this study were sometimes managed by the owner, and sometimes managed by a manager who was employed by the owner. In order to avoid cross-reference between terms, I hereafter use the term “manager” to refer to the person responsible for management decisions and actions on the PLCA. “Manager objectives” and “owner objectives” are thus considered synonymous (see Chapter 2 for an assessment of this assumption).

### 1.3 Thesis outline

In this thesis I propose that insight into the economic and ecological sustainability of the commercial private land conservation industry can be gained through cognizance that PLCAs are social-ecological systems. I predict that PLCA profitability and ecological management practices are driven by multi-scale interactions between natural resource systems, natural resource managers and their organizations, regional policies, and national and international tourist markets.

The first objective of this research is to investigate *if*, *how* and *why* commercial PLCA managers meet their financial objectives. In order to achieve this objective, I ask three key questions:

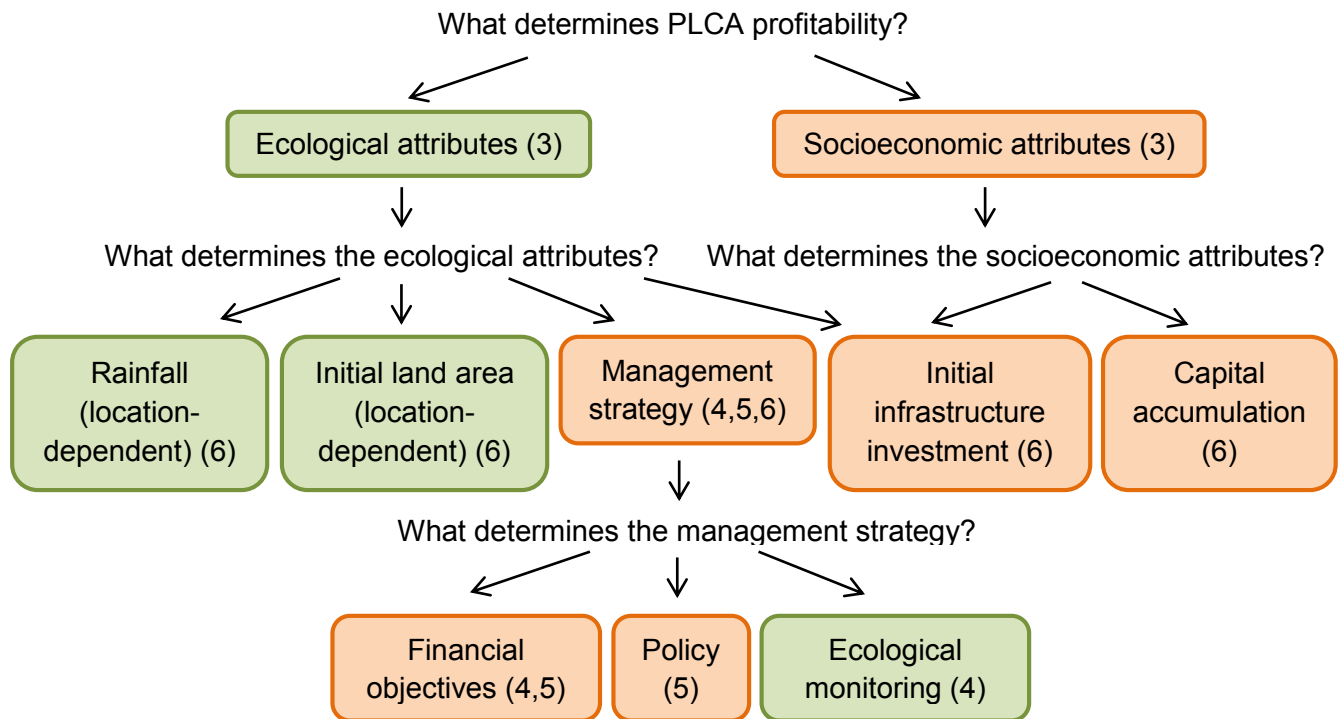
1. Are PLCA managers with financial objectives generating a profit? (Addressed in Chapter 3)
2. How do socioeconomic (e.g. accessibility, price, infrastructure and activities) and ecological (e.g. number and abundance of large mammal species) characteristics of a PLCA influence its revenue-generating capacity and profitability? (Addressed in Chapters 3, 4 and 5)
3. Are PLCA managers able to adapt their business strategies in order to achieve their financial objectives, and do adopted management strategies influence their ability to adapt? (Addressed in Chapter 6)

The second objective of this research is to investigate *if*, *how* and *why* commercial PLCAs adopt unsustainable ecological management practices. In order to achieve this objective, I ask three key questions:

1. Do PLCAs stock extralimital species or unsustainable numbers of game or predators? (Addressed in Chapters 4 and 5)
2. Do managers implement ecological management strategies that reduce natural ecological variability on their PLCAs, and does this result in higher game and predator richness and abundance? (Addressed in Chapter 4)
3. Do managers' financial objectives and/or ecological monitoring practices influence their ecological management strategies and outcomes, and do policies related to ecological management on PLCAs facilitate sustainable management? (Addressed in Chapters 4 and 5)

Chapter 2 provides a description of the study region (the Western and Eastern Cape Provinces of South Africa), the study site selection process, and the general methods used in this thesis. The business strategies adopted by PLCA managers are categorized in Chapter 3, and I undertake the first large-sample empirical assessment of the drivers of profitability on PLCAs (Fig.

4). Theories from organizational science are applied to understand patterns of diversity in adopted business models, and the likely long-term financial viability of PLCAs is interpreted in light of their financial objectives. This chapter illustrates the (largely ignored) relevance of organizational theories to social-ecological system analysis.



**Fig. 4.** Logic tree illustrating the hypothesized drivers of Private Land Conservation Area (PLCA) profitability and management, tested in this thesis. Bracketed numbers indicate the chapter(s) that addresses each driver. Social drivers are illustrated in orange and ecological/biophysical drivers are illustrated in green.

Ecological management strategies on PLCAs are assessed in Chapter 4. I quantify relationships between financial objectives, ecological monitoring, ecological management strategies, and ecological and financial outcomes (Fig. 4). Quantified ecological outcomes include game stocking rates and the presence of extralimital species. Social-ecological systems theory on the long-term consequences of managing ecological variability is used to make predictions regarding the ecological sustainability of alternative management strategies. The importance of manager action-outcome feedbacks as determinants of sustainability is discussed.

In Chapter 5 I focus specifically on the management of large predators on PLCAs. Theory on scale mismatches in social-ecological systems is applied to investigate whether regional

policies pertaining to large predator management and PLCA managers' financial objectives influence the sustainability of observed stocking rates of large predators, and the resultant ecotourism revenues generated from national and international tourists (Fig. 4).

Patterns in PLCA profitability and management are described in Chapters 3 to 5 using empirical ecological and financial data pertaining to a single year on surveyed PLCAs (2013). In order to test hypothesized mechanisms driving these patterns, I develop a mechanistic model of a PLCA in Chapter 6. I develop the model using simple rules for game and predator population dynamics relative to rainfall and land area (which are dependent on a given location's climate and land price, respectively), infrastructure and management strategies, and PLCA socioeconomic development options over time relative to accumulated capital and initial infrastructural constraints. I apply theories from organizational science to explore whether initial conditions (rainfall, land area, infrastructure) and ecological management strategies influence the ability of PLCAs to adapt their business models to meet their financial objectives over time (Fig. 4).

In Chapter 7 I synthesize my findings in light of my aim and objectives. I describe how PLCA profitability and management practices are driven by multi-scale, social-ecological interactions. I use insights gained from the unique application of organizational sciences to social-ecological system analysis to discuss how organizational theories could be better embedded within social-ecological systems theory. I emphasize that answering the “*why*” questions posed by this thesis necessitates understanding manager action-outcome feedbacks; an important but ill-considered driver of sustainability in social-ecological systems. I outline the practical implications and recommendations of my study, and highlight emergent opportunities for further research.

Chapters 3 to 6 have been written as stand-alone papers to facilitate publication of this research (refer to “*Papers arising from this thesis*”). While I have removed repetition in concepts and methods as much as possible for the purposes of this thesis, in some cases this repetition is essential for the readability of each chapter.

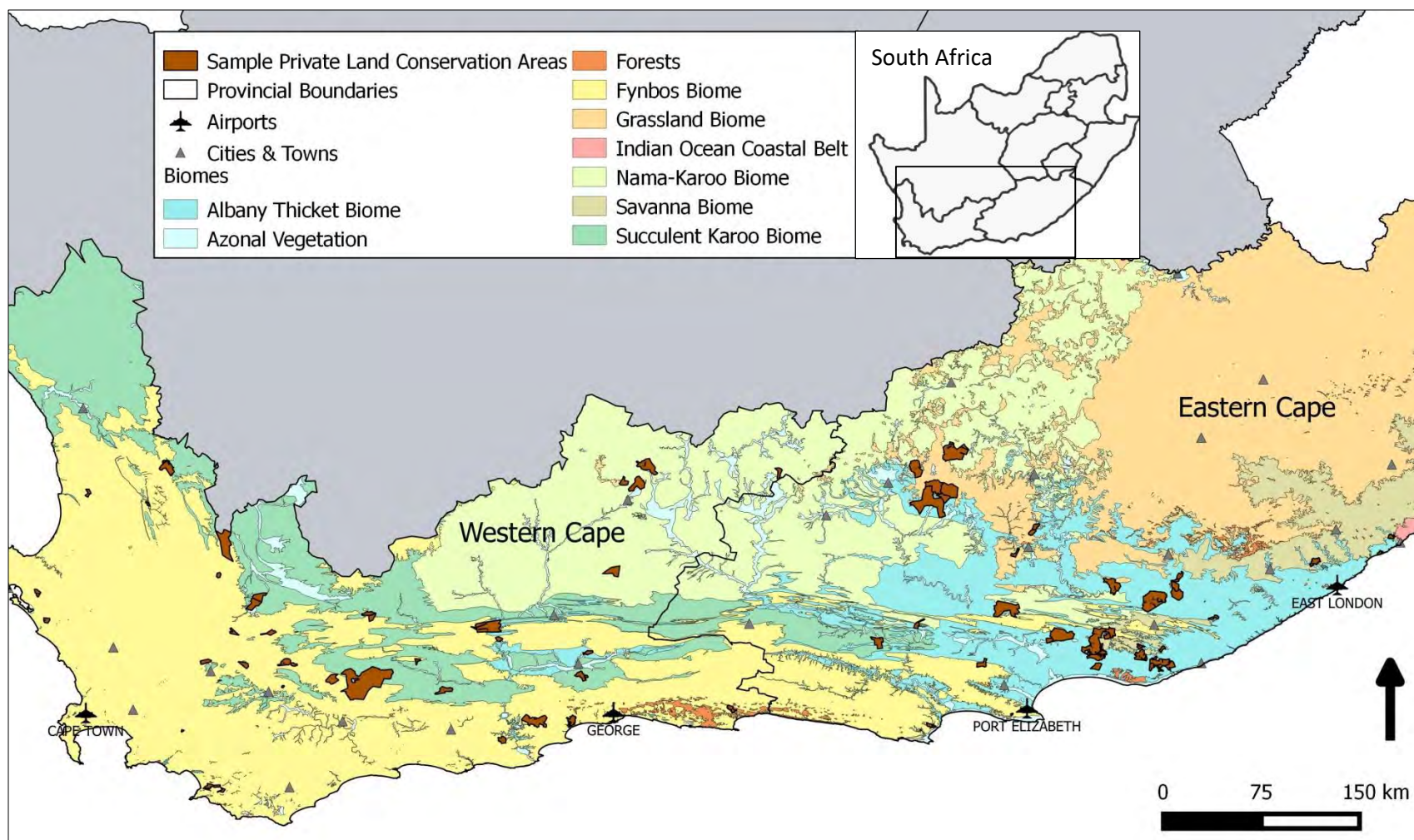
### 2.1 Study region and study site selection

This thesis focusses on commercial Private Land Conservation Areas (PLCAs) in a region that has seen substantial growth in this industry over the past 20 years but remains poorly understood; the Western and Eastern Cape Provinces of South Africa. The Western Cape Province is 130,000 km<sup>2</sup> in extent and characterized by the Fynbos, Nama-Karoo, Succulent Karoo and Thicket biomes (Fig. 1). It is a region of high biodiversity value, with the Cape Floristic Region and the Succulent Karoo being two of the world's 25 biodiversity hotspots (Myers et al. 2000). Cape Town is the largest city and five national roads pass through the province. The province has two airports: Cape Town International and George National (Fig. 1).

The Eastern Cape Province is 169,000 km<sup>2</sup> in extent. It is the only province to contain all three of South Africa's global biodiversity hotspots (Cape Floristic Region, Succulent Karoo and Maputoland-Pondoland-Albany; Myers et al. 2000), with the Grassland, Nama-Karoo, Savanna, and Forest biomes also occurring in the province (Fig. 1). The largest city is Port Elizabeth and four national roads pass through the province. The province has two airports: Port Elizabeth International and East London National (Fig. 1).

A list of commercial PLCAs in the Eastern and Western Cape Provinces of South Africa was compiled using the South African Protected Area Database (Department of Environmental Affairs 2016). This list was augmented by the list of PLCA managers interviewed by Baum (2016), as well as online searches using keywords such as “private”, “game”, “nature” and “reserve”. I included sites that met the PLCA definition (see section 1.2.3), and provided diversity in size, geographical location, ecology (richness and type of vegetation, game, megaherbivores and large predators), legal status, available facilities and marketed activities. Game include equid and bovid species, such as plains zebra *Equus quagga* and springbok *Antidorcas marsupialis*. Megaherbivores are herbivores weighing over 1000 kg; African megaherbivores include black rhinoceros *Diceros bicornis*, elephant, giraffe, hippopotamus *Hippopotamus amphibius* and white rhinoceros *Ceratotherium simum*. Members of the large African predator guild include cheetah *Acinonyx jubatus*, brown hyaena *Parahyaena brunnea*, leopard *Panthera pardus*, lion *Panthera leo*, spotted hyaena *Crocuta crocuta* and wild dog *Lycaon pictus*.





**Fig. 1.** Map of the Eastern and Western Cape Provinces of South Africa, depicting biomes, cities and airports. Study site Private Land Conservation Areas are depicted in brown.



A list of 412 potential PLCA study sites was compiled, of which contact details could be sourced for 151 that appeared to meet the commercial PLCA definition (76 in the Eastern Cape and 75 in the Western Cape). Given time constraints on data collection, 75 study PLCAs were selected randomly from this list, ensuring similar sample sizes from both provinces. Owners and/or managers of selected PLCAs were contacted by telephone, and face-to-face interviews were arranged with those who agreed to participate. Of this initial selection, 14 PLCAs either declined requests for interviews or it became evident during the interview that they had insufficient time to complete the questionnaire (see section 2.2) or did not meet the commercial PLCA definition. An additional 11 PLCAs were contacted, resulting in a final sample size of 72 PLCAs (Fig. 1).

## **2.2 Data collection**

In order to meet the objectives outlined in Chapter 1, I developed a questionnaire to be answered by the owners or managers of study site PLCAs. The questionnaire was circulated to specialists for recommendation, after which ethics approval was obtained (University of Cape Town Faculty of Science Research Ethics Committee Approval Code FSREC 11– 2014). The questionnaire was then tested in two pilot interviews and some modifications were made.

The final questionnaire comprised of four sections (see Questionnaire 1), each of which included both structured, categorical questions and open-ended questions. The first section included general details on the PLCA: size, property details (farm numbers/names), age, prior land use, ownership details, fencing etc. It asked for details of the interviewee: position, duration of employment to-date, prior experience and education. Interviewees were asked to fill in a timeline of notable changes in PLCA ownership, size, objectives, business strategies etc. The remainder of this section related to (a) the objectives for the PLCA, and (b) how important various ecological, infrastructural, location, activity, target market and marketing attributes were to achieving these objectives. When non-owners (i.e. employed managers) were interviewed, if they stated that they were unable to answer these questions then the PLCA owner was contacted. The second section related to financial attributes of the PLCA in the 2013/2014 financial year: pricing, overnight and day visitor capacities and occupancy rates, staff numbers, revenues and operating costs, financial requirements and thresholds. The third section related to the ecological management of the PLCA: how the vegetation, game and predators were managed. Interviewees were asked if they undertook any monitoring or research on the PLCA, and what types of information guided their management

decisions. Species lists, game counts (for 2013 or the closest year prior to this), maps and management plans were requested. Finally, information was obtained on social interactions with other conservation organizations.

I undertook semi-structured interviews with the owners or managers of 72 PLCAs between April 2014 and February 2015. Interviews mostly took place on PLCAs, though several took place in an alternative location, such as a coffee shop. Interview duration ranged from one to three hours and all interviews were conducted in English. The questionnaire was presented to all interviewees by means of an introductory statement that covered the following points: (a) the identity and affiliation of the interviewer; (b) the purpose of the study and its importance; and (c) assurance of the anonymity of the study participants and any information they provided during the interview (Pasquini 2007). All interviews were audio recorded and written notes were made during the interview. Open-ended questions were later transcribed.

Subsequent to the interview, details of properties comprising each PLCA were used to identify each PLCA in the South African cadastral farm boundary data (AfriGIS 2013). Maps of each PLCA were thereafter created in ArcGIS 10, and used in all subsequent spatial analyses. PLCA legal status was verified using the provincial gazettes and stewardship databases.

Study site PLCAs were owned by either individuals or corporations. I interviewed 29 non-owner managers and 43 owners. I performed Fisher's tests to assess whether non-owners and owners differed in their stated objectives for the PLCA. There was no difference in the relative number of owners and managers that rated profit generation as an important (Likert rating  $> 3$ , see Questionnaire 1) vs. unimportant (Likert rating  $\leq 3$ ) objective (*Fisher's exact*  $p = 0.3$ ), nor was there a difference in the relative number of owners and managers that rated conservation as an important vs. unimportant objective (*Fisher's exact*  $p = 0.99$ ). All analyses were performed in the statistical programme R (R Development Core Team 2016) at a significance level of  $\alpha = 0.05$ . Managers' objectives and owners' objectives are therefore considered as synonymous in this thesis.

**Questionnaire 1.** Research questionnaire for the managers of study site Private Land Conservation Areas (Note: additional writing space, present in the original version, has been removed here)

Park code \_\_\_\_\_ Date and duration \_\_\_\_\_

### 1. Private protected area objectives and strategies questionnaire

#### 1.1 Personal data

Name code \_\_\_\_\_

Position in the park \_\_\_\_\_

Education \_\_\_\_\_

When did you join the park? \_\_\_\_\_

Number of years of experience in park management \_\_\_\_\_

#### 1.2 Park data

When was the park established and opened to the public? \_\_\_\_\_

How big is the park? \_\_\_\_\_

What are the names / numbers of the farm portions that make up the park? \_\_\_\_\_

Who owns the park? \_\_\_\_\_

What nationality is/are the owners? \_\_\_\_\_

Has ownership changed since park establishment? \_\_\_\_\_

What was the land use of the area prior to park establishment? \_\_\_\_\_

Is the park fully / partially game fenced? \_\_\_\_\_

#### 1.3 Please describe the objectives of the park \_\_\_\_\_

#### 1.4 Can you describe your strategy for achieving these objectives?

\_\_\_\_\_

#### 1.5 Have the objectives of the park changed since its inception? If so, how? \_\_\_\_\_

#### 1.6 Please rate the following objectives on a scale of 1 (not relevant) to 5

(very important):	1	2	3	4	5
To make a profit	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Conservation / protecting nature	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Education	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Research facilitation	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
The owner's personal enjoyment / family history	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#### 1.7 If conservation is an objective of the park, is there a specific aspect of conservation that the park is focused on? (For example, endangered / rare species, large mammals, vegetation etc.)

\_\_\_\_\_

#### 1.8 What do you perceive to be the most disturbing impacts / threats to the park's objectives? \_\_\_\_\_

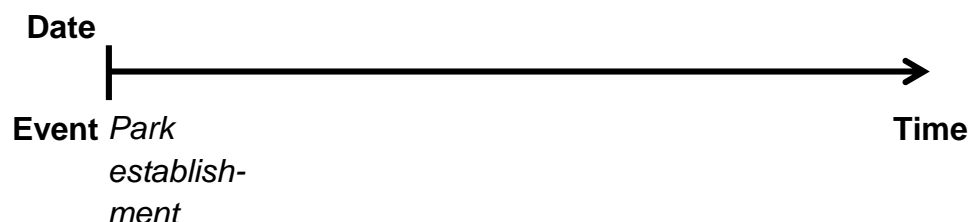
#### 1.9 Please rate, on a scale from 1 (not relevant) to 5 (very important), the following problems in contributing to general failure in a park like this one:

	1	2	3	4	5
Ecological problems	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

	1	2	3	4	5
Social problems	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Economic problems	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

Why do you say this? \_\_\_\_\_

1.10 Below is a timeline of your park, starting when the park was established. Please indicate on this timeline any changes in park ownership, size, objectives, business strategies, and anything else that you see as important in describing how your park has developed and changed.



1.11 Please rate the following attributes of the park in terms of their importance for achieving the park's objectives, on a scale of 1 (not relevant) to 5 (very important):

1.11.1 *Ecological attributes*

	1	2	3	4	5
Megaherbivores (giraffe, elephant, rhino, hippo)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Large predators (lion, leopard, cheetah, wild dog, hyaena)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Large mammals (e.g. antelope, zebra)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Small mammals, reptiles, invertebrates	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Birds	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Fish	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

	1	2	3	4	5
A specific species _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Vegetation	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Rivers / dams	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Landscape features (e.g. waterholes, viewing points): _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

1.11.2 *Infrastructure, location and economic attributes*

	1	2	3	4	5
Accommodation	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Restaurant / catering facilities	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Self-catering facilities	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Conference centre / event facilities	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Day visitor facilities	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Curio shop	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
An attraction nearby the park (e.g. town, national park etc.), please specify _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

1.11.3 *Target market attributes*

	1	2	3	4	5
International visitors	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
National visitors	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Rate the importance of visitors from the following international origins:					
European	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Asian	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Russian	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
North American	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Australian	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
African (excluding South African)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
South American	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

What are the three most important origins of local visitors?

	1	2	3	4	5
1. _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
2. _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
3. _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#### 1.11.4 Activities

	1	2	3	4	5
Guided game viewing	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other guided tours _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Self-drive game viewing	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Walking / hiking / climbing	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Driving off-road / 4x4'ing	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Watersports (canoeing, boating, swimming)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Game handling	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Birding	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Fishing	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Hunting	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Volunteering	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Events (e.g. weddings, conferences)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Environmental education	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Spa treatments	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Child care / entertainment	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Game sales	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Natural product sales (excluding game)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Agriculture / livestock farming	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

#### 1.11.5 Park marketing

	1	2	3	4	5
Website	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Advertisements	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

	1	2	3	4	5
Tour operators / agents	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Social media	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Word of mouth	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

Please provide the five most important key words used to market your

park: (1) \_\_\_\_\_ (2) \_\_\_\_\_

(3) \_\_\_\_\_ (4) \_\_\_\_\_ (5) \_\_\_\_\_

## 2. Private protected area financial questionnaire

2.1 What are the rates charged for a night's accommodation per person, in each accommodation type?

Accommodation Type	Star rating	High season ( _____ )	Low season ( _____ )

Are meals included in accommodation rates? Yes ☐ No ☐

What activities are included in accommodation rates? \_\_\_\_\_

2.2 What are the rates charged for park entrance fees / day visitors:

\_\_\_\_\_

2.3 What are the rates charged for functions?

\_\_\_\_\_

2.4 What are the costs of additional activities?

1. \_\_\_\_\_ 2. \_\_\_\_\_

3. \_\_\_\_\_ 4. \_\_\_\_\_

2.5 For overnight guests, how many can you accommodate at any one time? \_\_\_\_\_

2.6 For day visitors, how many do you allow to visit at any one time?  
\_\_\_\_\_

2.7 What was your occupancy rate for overnight guests in 2013?  
\_\_\_\_\_

2.8 How many day visitors did you get in 2013? \_\_\_\_\_

2.9 When is your high, medium and low season, according to visitation rates?  
High \_\_\_\_\_ Medium \_\_\_\_\_ Low \_\_\_\_\_

2.10 Do you collect data about tourism in your park and are you able / willing to make these available to us? Yes ☐ No ☐

2.11 How many staff members do you employ for:  
a. The reserve \_\_\_\_\_ b. The lodge \_\_\_\_\_ c. Other \_\_\_\_\_

2.12 In which category is the total revenue which the park received in the last (2013/2014) financial year:

None ☐ <R100 000 ☐  
R100 000 to R200 000 ☐ R200 000 to R500 000 ☐  
R500 000 to R1 million ☐ R1 million to R5 million ☐  
R5 to R10 million ☐ >R10 million ☐

Actual amount: \_\_\_\_\_

Can you provide figures for the previous years? Yes ☐ No ☐

2.13 Please detail the relative proportions (and/or amounts) of the park's revenue that come from:

	Percent	/	Amount
Ecotourism	_____		_____
Education groups	_____		_____
Volunteer ecotourism	_____		_____
Event hosting	_____		_____
Researchers	_____		_____
Biltong hunting	_____		_____
Trophy hunting	_____		_____
Game sales	_____		_____
Farming	_____		_____
Other _____	_____		_____

Are there any additional revenue sources, such as money from the owner, funding / donations, ecosystem service payments etc.?

Yes ☐ No ☐ Details \_\_\_\_\_

2.14 In which category is the total running cost incurred by the park in the last (2013/2014) financial year:

None ☐ <R100 000 ☐  
R100 000 to R200 000 ☐ R200 000 to R500 000 ☐  
R500 000 to R1 million ☐ R1 million to R5 million ☐  
R5 to R10 million ☐ >R10 million ☐

Actual amount: \_\_\_\_\_

Can you provide figures for the previous years? Yes ☐ No ☐

2.15 Please detail the relative proportions (and/or amounts) of the park's costs that are attributable to:

	Percent	/	Amount
--	---------	---	--------

Maintenance (lodge, roads, fences, vehicles)		
Lodge staff salaries (incl. field guides)		
Reserve staff salaries		
Game purchases		
Game management (e.g. veterinary bills, food etc.)		
Ecological research and monitoring		
Marketing and administration		
Insurance		
Food and beverages		
Fuel		
Rates		
Permits / licenses		
Other		

2.16 In which category was the total start-up cost incurred by the park:

- None ☐ <R100 000 ☐  
 R100 000 to R200 000 ☐ R200 000 to R500 000 ☐  
 R500 000 to R1 million ☐ R1 million to R5 million ☐  
 R5 to R10 million ☐ >R10 million ☐

Actual amount: \_\_\_\_\_

What percentage of this start-up cost has been paid off? \_\_\_\_\_

2.17 Did the park in the last (2013/2014) financial year:

Make an operating profit ☐ loss ☐ broke even ☐

2.18 What percentage of park profit do you reinvest in the park?

\_\_\_\_\_

2.19 In the last five years has the financial situation of the park:

Improved ☐ Stayed the same ☐ Worsened ☐

2.20 Is the park the owner's only source of income? Yes ☐ No ☐

2.21 What are the owner's current and future requirements, in terms of annual financial output? \_\_\_\_\_

2.22 Please tell me what the owner would do in the following situations:

	<b>Sell park</b>	<b>Change land use</b>	<b>Other</b>
The park: made a loss for the next 5 years	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Details _____			
made a loss for the next 10 years	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Details _____			
made a loss for the next 20 years	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Details _____			
only broke even for the next 5 years	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Details _____			
only broke even for the next 10 years	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Details _____			
only broke even for the next 20 years	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Details _____			

2.23 Under what circumstances may the owner decide to sell the park or change its land use? \_\_\_\_\_

### 3. Private protected area management questionnaire

3.1 Please describe your general approach to management on the park \_\_\_\_\_

3.2 Do you have a management plan for your park? Yes ☐ No ☐

If yes, who developed it and when? \_\_\_\_\_

Do you update your management plan? Yes ☐ No ☐

If yes, who updates it and how often? \_\_\_\_\_

Would you be willing to provide me with a copy? Yes ☐ No ☐

3.3 How often has the manager position been newly filled in the last five years? \_\_\_\_\_

3.4 Does the park employ or make use of an ecologist / conservationist?  
Yes ☐ No ☐ If yes, please provide details (qualification and how long this position has existed / how frequently the person is consulted if not employed etc.) \_\_\_\_\_

3.5 Do you perceive hunting and ecotourism to:  
Conflict with each other ☐ Complement each other ☐  
Not affect each other ☐  
If you provide both activities, are they spatially/temporally separated on your park? Yes ☐ No ☐

3.6 Do you do game counts? How and how often? \_\_\_\_\_  
Would you be willing to supply me with current game count data / a species list for the park: Yes ☐ No ☐  
Can you provide counts for previous years? Yes ☐ No ☐  
Which large predators occur on the park? Do they occur in a subsection of the park, and if so, how big is this subsection?  
\_\_\_\_\_

3.7 Do you have GIS layers for your park (vegetation, roads, infrastructure etc.)? Yes ☐ No ☐

Would you be willing to share this information with me? Yes ☐ No ☐

3.8 Do you actively manage the following aspects of your park:

3.8.1 **Vegetation:** Yes ☐ No ☐  
How? \_\_\_\_\_  
\_\_\_\_\_

Do you:	Regularly/ continuously /always	Seasonally each year	Irregularly (once/twice each yr)	< once/ yr	< once/ 5 yrs	Never
---------	---------------------------------------	-------------------------	--	---------------	---------------------	-------

Use prescribed fire

<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
--------------------------	--------------------------	--------------------------	--------------------------	--------------------------	--------------------------

Clear alien invasives

<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
--------------------------	--------------------------	--------------------------	--------------------------	--------------------------	--------------------------

Restore natural vegetation / control soil erosion

<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
--------------------------	--------------------------	--------------------------	--------------------------	--------------------------	--------------------------

Cut / irrigate natural vegetation

<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
--------------------------	--------------------------	--------------------------	--------------------------	--------------------------	--------------------------

Other \_\_\_\_\_

<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
--------------------------	--------------------------	--------------------------	--------------------------	--------------------------	--------------------------

Why do you manage the vegetation?  
\_\_\_\_\_  
\_\_\_\_\_

3.8.2 **Game:** Yes ☐ No ☐  
How? \_\_\_\_\_  
\_\_\_\_\_



Do you:	Regularly/ continuously /always	Seasonally each year	Irregularly (once/twice each yr)	< once/ yr	< once/ 5 yrs	Never
Introduce game	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sell game	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Hunt	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Contracept	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Provide additional food	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Inoculate / dip against disease	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Veterinary treatment of diseases / injuries	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Antipoaching activities	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Use of enclosures / bomas	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Use of artificial waterholes	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

Why do you manage the game?

---

3.8.3 **Predators:** Yes ☐ No ☐

How? \_\_\_\_\_

---

Do you:	Regularly/ continuously /always	Seasonally each year	Irregularly (once/twice each yr)	< once/ yr	< once/ 5 yrs	Never
Introduce predators	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sell predators	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Cull	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Contracept	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Provide additional food	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Inoculate / dip against disease	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Veterinary treatment of diseases / injuries	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Antipoaching activities	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Use of enclosures / bomas	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Use of artificial waterholes	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

Why do you manage the predators?

---

3.9 Please explain to me what information you generally use to inform the management of vegetation, game and predators. \_\_\_\_\_

3.10.1 How often do you use the following sources of information to make your decisions regarding vegetation, game and predator management on the park:

	Never	Occasionally	Mostly	Always	Details
Personal experience	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	_____
Consultation with other managers or experts	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	_____
The management plan	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	_____
Evidence from on-site monitoring or research	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	_____
Text books / manuals	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	_____
Scientific publications	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	_____
The park's current economic situation / cashflow / revenue generation	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	_____
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	_____

3.10.2 Do you perform any research on the park, what type, how and how often? \_\_\_\_\_

3.10.3 Do you perform any ecological monitoring on the park, what type, how and how often? \_\_\_\_\_

3.11 How many kilometers of roads and square meters of infrastructure do you have on the park? \_\_\_\_\_

Do you allow off road driving? Yes ☐ No ☐

#### 4. Private protected area interaction questionnaire

4.1 What other conservation entities do you interact with?

National Parks (NP): \_\_\_\_\_

Provincial Parks (PP): \_\_\_\_\_

Private Protected Areas (PPAs): \_\_\_\_\_

Organizations / Specialists: \_\_\_\_\_

4.2 How often do you interact with these entities?

	Weekly	Monthly	Biannually	Annually	< Annually
NP	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
PP	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
PPA	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Organizations / Specialists	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

4.3 On a scale of 1 (not relevant) to 5 (most important) please indicate your opinion with regards to the role that these entities play with facilitating:

	1	2	3	4	5
Marketing collaboration (in terms of ecotourism/hunting/wildlife trade)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Marketing competition	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Spread of ecological problems (e.g. diseases, alien invasive species)	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Control of ecological problems	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sharing of resources and equipment	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Sharing of wildlife knowledge and research	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>
Other _____	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>	<input type="checkbox"/>

4.4 Do you have any other comments? \_\_\_\_\_

## CHAPTER 3: MONEY AND MOTIVES: AN ORGANIZATIONAL ECOLOGY PERSPECTIVE ON PRIVATE LAND CONSERVATION

---

### Abstract

Analyses of institutions (rules, laws, traditions) and their relevance for conservation are increasingly common in conservation contexts. By contrast, the organizations that operate within the framework provided by institutions are less researched. I applied ideas from organizational ecology to understand the economic strategies of private land conservation areas (PLCAs), and their sustainability. The biophysical and socioeconomic characteristics of 72 commercial PLCAs in the Eastern and Western Cape Provinces of South Africa were used, via principal components and cluster analyses, to identify alternative business models. I found four distinct business models with different financial productivity and objectives. The most profitable models were (1) large ecotourism areas with many charismatic (megaherbivore/predator) and other (antelope) game species, expensive accommodation, and guided activities; and (2) small ecotourism areas with many charismatic game species, fewer other game species, short travel time from the nearest airport, guided activities and day visitors. The less profitable models were (3) hunting reserves, with 54% of managers seeking to generate profits but not doing so, creating a mismatch between financial objectives and financial returns; and (4) PLCAs with few game species and cheap accommodation/activities, which were similarly unprofitable although an absence of financial objectives limited mismatches to just 5%. Biophysical and socioeconomic incompatibilities between different business models make it difficult for PLCAs to change their business model if objectives are not met. Initial (and rational) choices of how to manage a natural resource can thus constrain future management options and the organization's ability to persist in a dynamic environment.

### 3.1 Introduction

Many conservation actions have come under criticism for being insufficient or ineffective, often as a result of limitations incurred by either the institutions (rules, laws, traditions) that regulate how conservation actions can be achieved or the organizations (governmental departments, businesses, societies, nonprofit groups) that undertake them. Analyses of *institutions* and their relevance for conservation are increasingly common in conservation contexts (Barrett et al. 2001), and recognition of the importance of institutions for conservation success is widespread in both social-ecological system analysis and conservation

science (e.g. Ostrom 1990; Anderies et al. 2004). Somewhat less attention has been paid to the role of *organizations*.

The scientific community has called for an assessment of the capacity of conservation organizations to adapt to changing conditions, and an identification of the drivers of persistence in this diverse global network (Larson et al. 2014; Armsworth et al. 2015). Given the importance of organizations for conservation, it seems strange that the existing body of theory relating to organizations has been largely ignored by conservation scientists. Of particular relevance is the field of organizational ecology, which has emerged from the application of ecological perspectives to the business environment. Organizational ecology seeks to explain how environmental (social, economic, political) conditions affect the relative abundance and diversity of organizations, and to understand the changing composition of organizations over time (Hannan & Freeman 1977; Baum 1999). In understanding the relative abundance and diversity of organizations, it is hypothesized that organizations become segregated into distinct clusters sharing a common “identity” when there are incompatibilities between organizational characteristics that restrict the combinations of characteristics that can emerge and persist (e.g. technological incompatibilities and transaction costs in manufacturing, construction, farming, and commercial industries; Hannan & Freeman 1986; Ruef 2000).

In considering changes in the composition of organizations over time, organizations may have difficulty adapting their identities efficiently to meet the demands of an uncertain, changing environment. Effective adaptation can be limited by high sunk (unrecoverable) costs and legal and economic barriers of exit and entry (which impede organizations leaving or entering an industry; Hannan & Freeman 1977). Organizational ecologists have argued that organizational survival is dependent on a high degree of reliability in the provision of services/activities, and accountability in management actions (Hannan & Freeman 1984; Hannan et al. 2004). The theory of structural inertia states that (a) organizations are often unable to adapt at an appropriate rate to emerging changes in their environment; and (b) frequent adaptation to constantly changing conditions can be maladaptive if it undermines the organization’s reliability and accountability (Hannan et al. 2004; Stieglitz et al. 2016). Organizations with identities that are “matched” with current conditions will persist, while “mismatched” organizations that incur limitations in their ability to adapt appropriately will ultimately disappear (Hannan & Freeman 1977).

Ideas from organizational ecology have significant potential for understanding the likely persistence and effectiveness of conservation organizations. In this chapter I apply an organizational approach to the topic of private land conservation, which is increasingly

important in global conservation efforts (Langholz & Lassoie 2001; Stolton et al. 2014). A significant conservation concern is whether private land conservation areas (PLCAs) will be able to effectively conserve biodiversity over suitably long time frames. This question reflects a core theme of organizational ecology: how do environmental conditions affect the relative abundance and diversity of organizations, and the ability of individual organizations to persist over time? Here I define persistence as the continued maintenance of a natural (untransformed) land cover, with at least current levels of biodiversity. Environmental conditions in this context include biophysical and socioeconomic conditions (e.g. climate and the tourism market, respectively).

Assessing the likely persistence of a PLCA requires cognizance of the motives, besides biodiversity conservation, behind its establishment and maintenance. An international assessment of PLCAs found motives to vary widely, including philanthropy, quality of life, business, and acquiring governmental financial incentives (Stolton et al. 2014). Many PLCAs have developed fund-generating activities such as ecotourism and hunting (Langholz & Lassoie 2001; Stolton et al. 2014). The motive underlying these activities is sometimes to offset PLCA costs, with other PLCA owners stating profit generation to be an important objective in-and-of-itself (Langholz et al. 2000; Pasquini et al. 2010a). Understanding the ability of such PLCAs to achieve their objectives therefore requires an assessment of the efficacy of PLCAs in generating profits.

In Latin America and sub-Saharan Africa in the 1990's, 59% of surveyed PLCAs were profitable (Langholz 1996). Financial models suggest that ecotourism has the potential to generate a greater return on investment than hunting in some southern African countries, while both activities fare poorly in others (Barnes & de Jager 1996; Barnes 2001; Absa Group Economic Research 2003). Consumptive uses of wildlife, such as meat sales and hunting, have nonetheless become important industries in southern Africa (Bond et al. 2004; Novelli et al. 2006).

Within the ecotourism industry, forest reserves in eastern Africa attracted fewer visitors than savanna game parks (Bayliss et al. 2014). Megaherbivores and large predators were the most popular species for international visitors to South Africa, though local visitors were more interested in smaller, rarer species and scenery (Lindsey et al. 2007; Di Minin et al. 2013; Hausmann et al. 2016). "High-end, low-volume" (high price per visitor, low number of visitors) ecotourism on private land has become a significant industry within southern Africa, targeting international tourists from high income countries (Bond et al. 2004; Magole & Magole 2011). South Africa also supports a strong domestic tourism market, with demand for "low-end"

(affordable) ecotourism opportunities (Bond et al. 2004). Visitor numbers to PLCAs are therefore not a function of ecological attributes alone, but also other biophysical as well as socioeconomic characteristics of the PLCA, including affordability, accessibility, and available facilities (Bayliss et al. 2014; De Vos et al. 2015). The availability of educational experiences such as guided tours can further influence the quality of visitor experience (Kerley et al. 2003).

Assessing the profitability of a PLCA therefore requires consideration of the adopted business model, as defined by available features and activities, both biophysical and socioeconomic. Organizational ecology defines an organization's identity according to its structural features and patterns of activity (Hannan & Freeman 1977); a PLCA's business model can be considered analogous to its identity. In organizational ecology, biophysical and socioeconomic incompatibilities between different organizational characteristics are interpreted as driving segregating processes that create distinct clusters, or business models, with different identities. Such incompatibilities are likely to be evident on PLCAs between certain combinations of biophysical and socioeconomic characteristics. For example, PLCAs that rely on large predator species to attract tourists are unlikely to support large-scale hunting operations because of unsustainable stresses on the game population and potentially negative feedback from non-hunting guests. PLCAs that offer a high-end, low-volume safari experience may not concurrently cater for high quantities of day visitors that would detract from this exclusivity. Similarly, PLCAs that are far from airports and cities are unlikely to attract high volumes of day visitors.

In this chapter I focus on two questions relating to the organizational ecology of PLCAs. First, do distinct PLCA business models exist, and why? For the reasons outlined above, I anticipate that biophysical and socioeconomic segregating processes will exist in the PLCA industry and that distinct clusters of PLCAs will be characterized by business models that reflect these incompatibilities. Second, if PLCA business models are indeed discontinuous, what proportion of PLCAs adopting different business models match current environmental conditions? For those PLCAs for which profit is an important objective, a match between business model and current conditions is demonstrated by a match between financial objectives and profitability. Organizational ecology suggests that PLCAs should incur structural inertia as a result of segregating processes and barriers of exit and entry. This prediction would be supported if I were to observe PLCAs with financial returns that do not match financial objectives, reflecting an inability to adapt effectively to current conditions. Observed mismatches must be interpreted with some caution because of the role of temporal variation; knowledge of thresholds in how long owners would be willing to finance losses is important

for assessing the likely long-term persistence of mismatched PLCAs, as many PLCA owners report additional income sources (Langholz 1996; Langholz et al. 2000; Pasquini et al. 2010a) that may buffer mismatches. I test my predictions using commercial PLCAs in the Western and Eastern Cape Provinces of South Africa, and relate my findings to conservation organizations and natural resource management more generally.

## **3.2 Methods**

### **3.2.1 Data collection**

Four categories of information were obtained during interviews with the managers of 72 PLCAs in the Western and Eastern Cape Provinces of South Africa (Chapter 2), and from additional sources, as detailed in Table 1.

(1) PLCA specifications: Information on PLCA age, location and names of included farms was obtained.

(2) Objectives: The conservation and financial motives of the PLCA were assessed by asking each manager to rate protecting nature and profit generation as PLCA objectives on a Likert scale from one (not important) to five (very important). In order to identify potential financial thresholds, managers were asked (a) if an external income source contributed to funding the PLCA and (b) what actions would be taken in hypothetical situations where they did not achieve the PLCA's financial objectives in the next 5, 10, and 20 years. These actions were thereafter grouped into "no action" (finance the PLCA from external income sources), "sell the PLCA" or "try to adapt" (e.g. change the land use, sell game).

(3) Finances: Managers were asked whether the PLCA made an operating profit or loss in the 2013/2014 financial year, where an operating profit is a positive EBITDA figure (Earnings Before Interest, Tax, Depreciation and Amortization). Managers from 69 PLCAs answered this question. 52 managers further provided an EBITDA value for the 2013/2014 financial year. EBITDA (hereafter referred to as "income" or "profitability") is obtained from a business' income statement and is a commonly used metric for comparing incomes between businesses because it eliminates the effects of financing and accounting decisions and collections of assets.

Current market value for each PLCA property was calculated from the local municipality general valuation rolls for 2013. A general valuation roll is a legal document produced every four years according to The Municipal Property Rates Act 6 (2004), which assigns a market value to all properties in a municipality, accounting for both the land and the infrastructure. I calculated the current game value for all PLCAs from game count data, using

average game auction prices for each species sold in South Africa in 2013 (The Unit for Environmental Science and Management, North West University, unpublished data). Due to the diversity of counting techniques used and the diversity of habitats, no visibility correction factors were assigned to count data. Furthermore, I excluded smaller antelope species that are notoriously difficult to count, such as common duiker *Sylvicapra grimmia* and steenbok *Raphicerus campestris*. Game data were therefore likely to be undervalued across PLCAs, but sufficient for relative comparisons between PLCAs.

**Table 1.** Details and sources of data obtained for each Private Land Conservation Area (PLCA). Square brackets indicate characteristic names referred to in the results.

Data type	Details	Source
PLCA specifications	Names/numbers of farm portions comprising the PLCA Age since opened to the public Location	Interview with manager, and PLCA map (see Chapter 2)
PLCA objectives	Likert scale ranking of the importance of (a) protecting nature and (b) profit generation as a PLCA objective Other income source (Y/N) Actions to be taken if financial objectives not met in the next 5, 10, 20 years (categorical)	Interview with manager
PLCA finances	Operating profit made in the 2013/2014 financial year (Y/N) [profitability] Income for the 2013/2014 financial year [property value] Sum of land and improvement (infrastructure) valuations for each farm portion comprising the PLCA [game value] Total value of game [ROI] Return on investment	Interview with manager, and reference to the PLCA income statement and game count, local municipality general valuation roll (2013), North West University (unpubl. data)
PLCA characteristics – <i>Biophysical</i>	[size] Size (ha) [chari_game] Number of “charismatic” game species (megaherbivores and large predators) [other_game] Number of “other” game species (equids and bovids) [land_cover] Land cover diversity [elev_var] Elevation range (masl)	PLCA map (see Chapter 2) Interview with manager  South African National Land Cover Dataset Shuttle Radar Topography Mission Digital Elevation Data Version 4
– <i>Accessibility</i>	[travel_time] Travel time to nearest airport (minutes)	Google Maps
– <i>Affordability</i>	[price] Average daily price of visit (South African Rands)	Interview with manager
– <i>Infrastructure</i>	[bed_no] Number of beds available [cat.v.sc] Importance of restaurant/catering vs. self-catering facilities [stay.v.day] Importance of overnight vs. day visitor facilities	
– <i>Activities</i>	[guide.v.self] Importance of guided vs. unguided activities [eco] Proportion of revenue generated from ecotourism [hunt] Proportion of revenue generated from hunting [game_sales] Proportion of revenue generated from game sales [farm] Proportion of revenue generated from farming	
– <i>Market</i>	[int.v.loc] Importance of international vs. national visitors	



South African Rands were converted to United States Dollars using an average of the daily South African Reserve Bank exchange rate for the 2013/2014 financial year (\$1 = R10.00). Return on investment (ROI), a performance measure used to compare the efficiency of different businesses, was calculated by dividing income by the sum of property and game values. The average 2013 South African bond yield was obtained from the South African Reserve Bank, to compare ROI with a risk free rate of return (RFR: 7.7%).

(4) PLCA characteristics: I quantified a range of PLCA characteristics (biophysical-, accessibility-, affordability-, infrastructure-, activities- and target market-related) that could be used to distinguish different business models. Size was determined from PLCA maps, the numbers of “charismatic” game species (megaherbivores and large predators) and “other” game species (equid and bovid species) were counted using species lists, and a Shannon diversity index was used to calculate the abundance and diversity of natural land cover types in each PLCA as a metric for vegetation aesthetics, using the South African National Land Cover dataset and ArcGIS 10 (Van den Berg et al. 2008; De Vos et al. 2015). The standard deviation in elevation (masl) was used as a metric of topographical aesthetics, where a higher value illustrates greater diversity in elevation. Elevation raster data were obtained for South Africa (Shuttle Radar Topography Mission Digital Elevation Data Version 4) and the standard deviation in elevation (masl) was determined for each PLCA in ArcGIS 10.

Accessibility was measured as shortest travel time (in minutes) to the nearest international or national airport using Google Maps. Google Maps calculates the travel time between two points based on the fastest route taking into account traffic (near urban centers), the speed limit, and road speed index (a proxy for road condition; De Vos et al. 2015).

Affordability was calculated as average daily cost to visitor, between the most expensive accommodation with a full day of activities and the cheapest available option (either accommodation with no activities or a day’s activities with no accommodation). Number of available beds was determined. Activities were quantified by the proportional contribution to total revenue in the 2013/2014 financial year. Ecotourism represented the proportion of revenue generated from people visiting the PLCA to undertake ecotourism activities (including payments for entrance, activities, food and accommodation). Such activities included game- and nature-viewing drives and walks; game interaction opportunities; horse riding, quad biking and off-road driving; events and functions; and environmental education/volunteering programmes. Hunting represented the proportion of revenue generated from people visiting the PLCA in order to hunt or observe a hunt (including payments for accommodation, hunting fees and animals hunted). Game sales and farming represented the proportions of revenue generated

from the sale of live game and venison, and stock farming or small-scale agriculture, respectively. I did not have a quantitative measure of the importance of restaurant/catering facilities compared with self-catering facilities; the importance of overnight (i.e. accommodation) versus day visitor facilities; the importance of guided ecotourism activities compared with unguided (“self”) activities; or the importance of international visitors compared with national (“local”) visitors. Therefore, for each of these four metrics, managers were asked to rate the importance of each attribute to achieving their objectives, on a Likert scale from one (not important) to five (very important). Relative importance was then calculated as the importance of the attribute (e.g. restaurant) divided by the sum of the importance of both attributes (e.g. restaurant plus self-catering). Several guided and non-guided activities were listed (see Questionnaire 1); an average was taken to represent the importance of each category.

### 3.2.2 *Statistical analyses*

A principal component analysis was performed to explore correlations between PLCA characteristics (Table 1; R package: *vegan*; function: *rda*; Borcard et al. 2011; Oksanen et al. 2015). Prior to performing the principal component analysis, data were transformed where necessary to meet the assumptions of normality and all data were scaled. Three non-trivial components were identified (see results) using the broken-stick method (Jackson 1993), and are hereafter used to represent PLCA characteristics. A multiple linear regression was performed to assess whether PLCA characteristics were significant predictors of income (R package: *stats*; function: *lm*). Number of years commercially operated (“age”) was included as a predictor, to control for its potential influence on income. Predictor variables were examined for multicollinearity to avoid correlation among covariates. Plots of fitted and observed values and residuals were examined for deviations from the assumptions of homogeneity and normality. The adjusted coefficient of determination was used to assess model fit.

In order to assess whether PLCA characteristics were discontinuous, I performed an hierarchical agglomerative cluster analysis on PLCA characteristics, employing Euclidean distance and Ward linkages (R packages: *vegan* and *stats*; functions: *vegdist* and *hclust*; Ward 1963; Oksanen et al. 2015). I used a Mantel-based comparison as well as mean silhouette width to determine the number of distinct clusters (R package: *cluster*; functions: *daisy* and *silhouette*; Maechler et al. 2015).

Differences between the distinct PLCA business models identified by the cluster analysis (see results) were described by comparing differences in (a) mean principal component

scores and (b) mean values of the original 16 PLCA characteristics. I assessed whether there was a significant difference in the income, property value, game value and ROI between PLCAs adopting distinct business models. Comparisons were made using ANOVA and t-tests, and Kruskal-Wallis H and Mann-Whitney U tests, for normally and non-normally distributed characteristics, respectively. For each business model, differences in the number of PLCAs reporting protecting nature and generating profit to be important objectives (Likert scale rating  $> 3$ ) vs. unimportant (Likert scale rating  $\leq 3$ ) were assessed using Fisher's exact test. Statistical analyses were performed in the statistical programme R (R Development Core Team 2016) at a significance level of  $\alpha = 0.05$ . Sequential Bonferroni corrections were used to correct for multiple comparisons (Rice 1989).

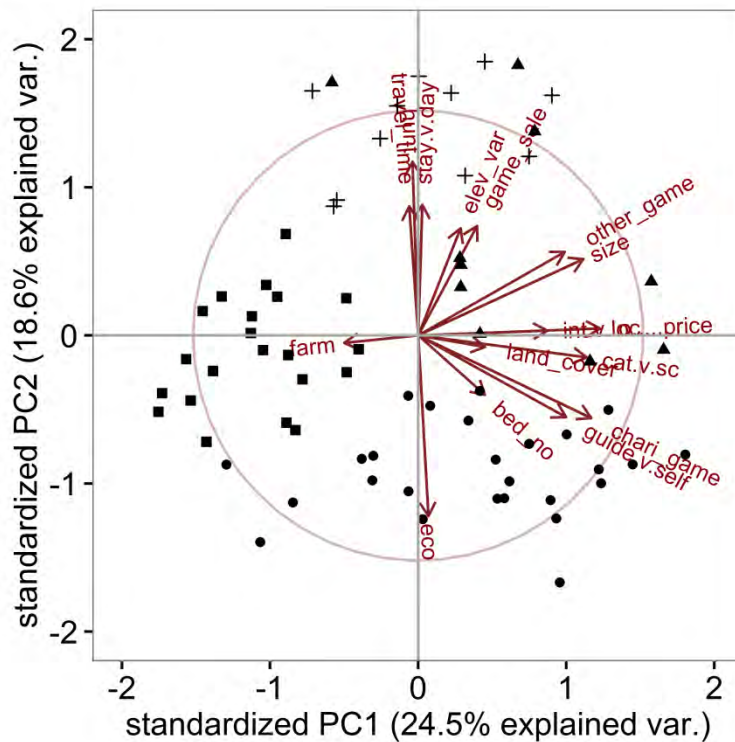
### 3.3 Results

Three non-trivial principal components accounted for 56.5% of the variation in 16 PLCA characteristics and explained 38.2% of the variation in income ( $F = 8.89$ ,  $n = 52$ ,  $p < 0.001$ ). Income (in \$100,000) increased with principal component one ( $\beta = 2.38 \pm 0.51$ ,  $t = 4.65$ ,  $p < 0.001$ ; Fig. 1) and decreased with principal component two ( $\beta = -1.89 \pm 0.56$ ,  $t = -3.37$ ,  $p = 0.002$ ; Fig. 1), while principal component three and age were not significant ( $t = -0.66$ ,  $p = 0.51$ ;  $t = 1.18$ ,  $p = 0.24$ , respectively).

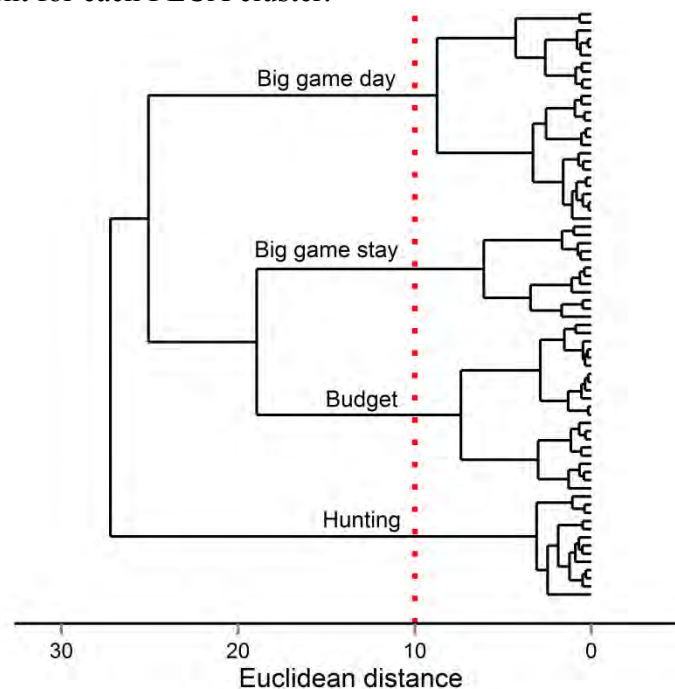
Two combinations of characteristics resulted in high incomes: (1) a large size, high number of charismatic and other game species, expensive accommodation and activities, the importance of a restaurant, guided activities, and international visitors; or (2) a small size, high number of charismatic game species but low number of other game species, low topographical diversity, short travel time, the importance of guided activities and day visitors, and revenue generated by ecotourism as opposed to hunting and game sales (Fig. 1; Appendix 3A).

Four distinct business models were identified ( $rM = 0.62$ ; average silhouette = 0.39; Fig. 2). All PLCA characteristics differed significantly between business models except land cover diversity and the proportion of revenue generated from farming (Table 2). "Hunting" reserves (18% of sample) were characterized by a large size, no charismatic game species, but large numbers of other game species; a low quantity of catered, intermediately-priced accommodation; a large proportion of revenue from hunting, followed by game sales; and the importance of international visitors (Fig. 1; Table 2).

"Budget" reserves (29%) were categorized by a small size, no charismatic game species and few other game species; cheap self-catering accommodation; the majority of revenue from unguided ecotourism; and the importance of local, overnight visitors (Fig. 1; Table 2).



**Fig. 1.** Biplot depicting the relative scores of 16 Private Land Conservation Area (PLCA) characteristics on the first two principal components (PCs). Data points indicate the scores of 72 PLCAs, with shapes corresponding to the four identified clusters (+ hunting; ■ budget; ▲ big game stay, ● big game day). Refer to Table 1 for characteristic descriptions. Refer to Appendix 3A for characteristic scores on each principal component and mean scores of each principal component for each PLCA cluster.



**Fig. 2.** Dendrogram depicting the Euclidean distances between 72 Private Land Conservation Areas (PLCAs), according to three principal components representing 16 PLCA characteristics. Four clusters are evident at a Euclidean distance of 10 ( $rM = 0.62$ ; average silhouette = 0.39).

“Big game stay” reserves (17%) were the largest PLCAs with the greatest topographical diversity, supporting multiple charismatic (“big”) game species and a large number of other game species. Expensive catered accommodation was on offer; with a large proportion of revenue generated from guided ecotourism and a smaller proportion from game sales and hunting. Overnight visitors were important (Fig. 1; Table 2).

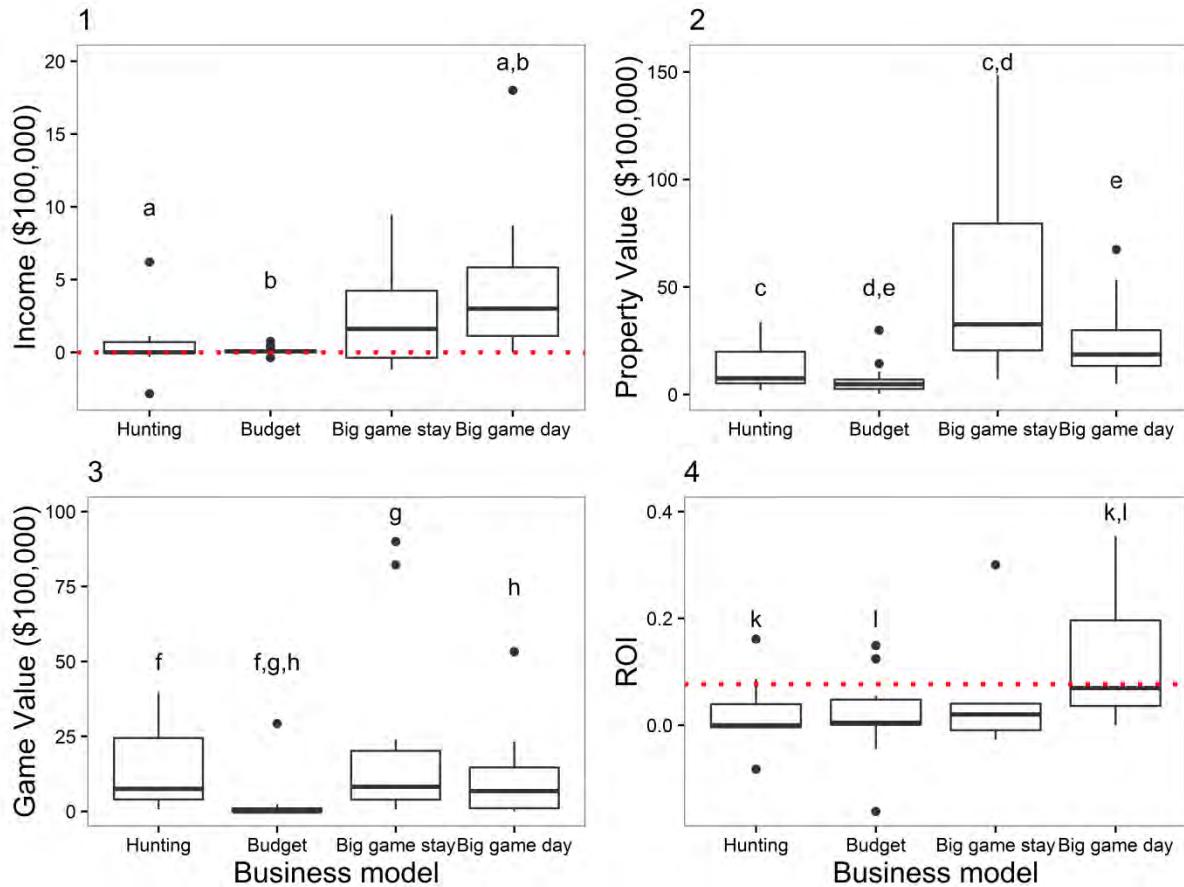
“Big game day” reserves (36%) were characterized by small size, low topographical diversity, multiple charismatic game species, an intermediate number of other game species and a short travel time. They offered intermediately-priced accommodation and activities and a restaurant; and the majority of revenue came from guided ecotourism. Both day and overnight international visitors were important (Fig. 1; Table 2).

**Table 2.** Average ( $\pm$ SE) values of 16 Private Land Conservation Area characteristics for each business model (\*bonferroni-corrected significant difference between business models). Refer to Table 1 for characteristic descriptions.

	Hunting	Budget	Big game stay	Big game day	Statistic	P
size (ha)	5179 ( $\pm$ 1288)	1557 ( $\pm$ 308)	17906 ( $\pm$ 3683)	2814 ( $\pm$ 555)	$K = 34.47$	<0.001*
chari_game	1 ( $\pm$ 0)	0 ( $\pm$ 0)	3 ( $\pm$ 1)	3 ( $\pm$ 1)	$K = 25.28$	<0.001*
other_game	16 ( $\pm$ 1)	6 ( $\pm$ 1)	14 ( $\pm$ 1)	12 ( $\pm$ 1)	$F = 14.40$	<0.001*
land_cover	0.72 ( $\pm$ 0.08)	0.64 ( $\pm$ 0.07)	0.90 ( $\pm$ 0.07)	0.80 ( $\pm$ 0.05)	$F = 2.63$	0.06
elev_var (masl)	86 ( $\pm$ 12)	97 ( $\pm$ 18)	179 ( $\pm$ 22)	52 ( $\pm$ 6)	$K = 22.07$	<0.001*
travel_time (min)	137 ( $\pm$ 15)	132 ( $\pm$ 11)	175 ( $\pm$ 15)	79 ( $\pm$ 7)	$F = 13.73$	<0.001*
price (R)	1611 ( $\pm$ 332)	428 ( $\pm$ 93)	2747 ( $\pm$ 496)	1810 ( $\pm$ 280)	$K = 29.29$	<0.001*
bed_no	15 ( $\pm$ 1)	61 ( $\pm$ 30)	56 ( $\pm$ 8)	47 ( $\pm$ 7)	$K = 23.55$	<0.001*
cat.v.sc	0.66 ( $\pm$ 0.05)	0.31 ( $\pm$ 0.05)	0.65 ( $\pm$ 0.07)	0.69 ( $\pm$ 0.04)	$K = 26.20$	<0.001*
stay.v.day	0.80 ( $\pm$ 0.03)	0.75 ( $\pm$ 0.02)	0.82 ( $\pm$ 0.01)	0.57 ( $\pm$ 0.03)	$K = 32.20$	<0.001*
guide.v.self	0.45 ( $\pm$ 0.05)	0.38 ( $\pm$ 0.04)	0.62 ( $\pm$ 0.05)	0.69 ( $\pm$ 0.03)	$K = 31.11$	<0.001*
eco	0.11 ( $\pm$ 0.03)	0.86 ( $\pm$ 0.05)	0.81 ( $\pm$ 0.09)	0.92 ( $\pm$ 0.03)	$K = 33.67$	<0.001*
hunt	0.68 ( $\pm$ 0.07)	0.05 ( $\pm$ 0.03)	0.10 ( $\pm$ 0.06)	0.01 ( $\pm$ 0.01)	$K = 45.83$	<0.001*
game_sale	0.21 ( $\pm$ 0.08)	0.01 ( $\pm$ 0.01)	0.08 ( $\pm$ 0.04)	0.04 ( $\pm$ 0.01)	$K = 13.22$	0.004*
farm	0.01 ( $\pm$ 0.01)	0.08 ( $\pm$ 0.05)	0.02 ( $\pm$ 0.01)	0.03 ( $\pm$ 0.03)	$K = 4.53$	0.21
int.v.loc	0.59 ( $\pm$ 0.03)	0.35 ( $\pm$ 0.03)	0.49 ( $\pm$ 0.03)	0.59 ( $\pm$ 0.02)	$K = 28.29$	<0.001*

Profitability differed between business models ( $K = 13.57$ ,  $p = 0.004$ ; Fig. 3), as a result of big game day reserves generating greater incomes than hunting and budget reserves ( $W = 22$ ,  $p = 0.002$ ;  $W = 29$ ,  $p < 0.001$ , respectively). There was no difference in profitability between hunting and budget reserves ( $W = 116.5$ ,  $p = 0.94$ ). Big game stay reserves did not differ in profitability from budget, hunting or big game day reserves ( $W = 60$ ,  $p = 0.42$ ;  $W = 40$ ,  $p =$

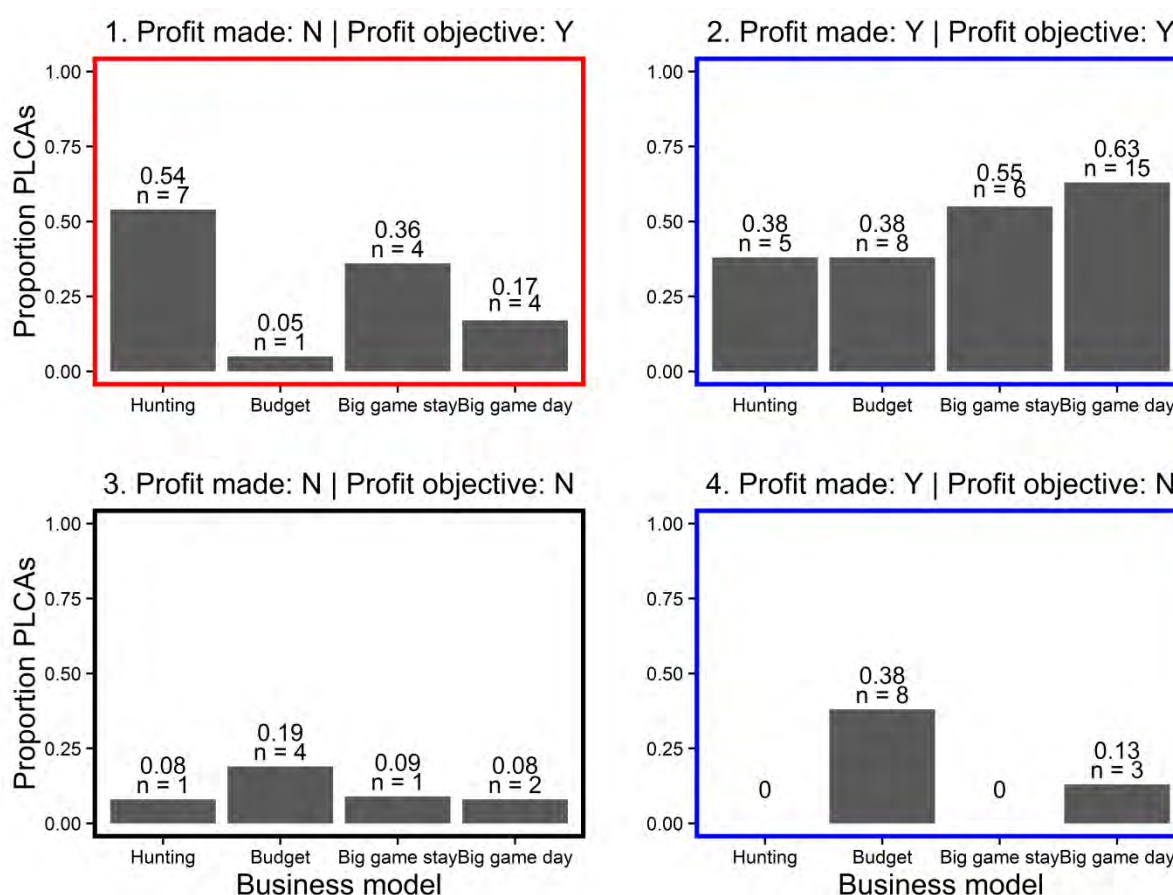
0.56;  $W = 67.5$ ,  $p = 0.28$ , respectively). While big game stay reserves generated, on average, the second greatest incomes, there was substantial variation in incomes (Fig. 3).



**Fig. 3.** Comparisons across Private Land Conservation Area business models of (1) income, (2) property value, (3) game value and (4) return on investment (ROI), for the 2013/2014 financial year. Lines, boxes, error bars, and circles show medians, interquartile ranges, minima and maxima (excluding outliers), and outliers (that deviate from the median by  $> 1 \times$  the interquartile range), respectively. Horizontal red dashed lines indicate (1) zero profit and (4) South African 2013 average bond yield of 0.077. Corresponding letters indicate significant differences between business models.

Property and game values differed between business models ( $K = 29.32$ ,  $p < 0.001$ ;  $K = 25.16$ ,  $p < 0.001$ , respectively; Fig. 3). Big game stay reserves were characterized by greater property values than hunting and budget reserves ( $W = 20$ ,  $p = 0.007$ ;  $W = 11$ ,  $p < 0.001$ , respectively), and big game day reserves were characterized by greater property values than budget reserves ( $W = 44.5$ ,  $p < 0.001$ ). Hunting, big game stay and big game day reserves supported game populations of higher value than budget reserves ( $W = 16$ ,  $p < 0.001$ ;  $W = 20.5$ ,  $p < 0.001$ ;  $W = 99$ ,  $p < 0.001$ , respectively). ROI differed between business models ( $K = 9.59$ ,  $p = 0.02$ , Fig. 3), with big game day reserves generating a larger ROI than budget and hunting reserves ( $K = 53$ ,  $p = 0.007$ ;  $K = 31$ ,  $p = 0.01$ , respectively). Big game day reserves were the only business model with a median ROI comparable to the RFR.

Protecting nature was rated an important objective on 83% of PLCAs, and this proportion did not differ significantly between business models (*Fisher's exact*  $p = 0.12$ ). The proportion of PLCAs that rated profit generation as an important objective differed between business models (*Fisher's exact*  $p = 0.004$ ). Just 43% of budget reserves rated profit generation as an important objective, significantly fewer than hunting (92%, *Fisher's exact*  $p = 0.004$ ), big game stay (91%, *Fisher's exact*  $p = 0.016$ ) and big game day (79%, *Fisher's exact*  $p = 0.011$ ) reserves. The red box in Figure 4 (pane 1) indicates PLCAs that stated profit generation was an important objective, but that were currently not generating a profit. 54% of hunting reserves fell within this box compared with 5%, 36% and 17% of budget, big game stay and big game day reserves, respectively. 94% of the PLCAs that were not currently achieving their financial objectives stated having another income source, usually the owner's personal funds.



**Fig. 4.** Proportion of Private Land Conservation Areas (PLCAs) within each business model that generated an operating profit vs. loss in the 2013/2014 financial year, and rated profit generation as an important vs. unimportant objective. Proportions and sample sizes (n) are indicated above each bar. Box colours indicate extent of mismatch between actual finances and financial objectives: match (blue: panes 2 and 4), potential mismatch long-term (black: pane 3) and mismatch (red: pane 1).

If PLCAs that were not currently meeting their financial objectives did not meet these objectives within the next ten years, 38% of managers said the PLCA would be sold and 43.5% would try to adapt their business model. Suggested adaptations included downscaling and retrenching staff, increasing hunting and game sales, breeding more exotic/valuable game, offering specials to attract more people, closing high-end ecotourism lodges and becoming a hunting operation, and removing costly predators. Suggested adaptations on 12.5% of PLCAs included changing the land use to a wind farm or livestock farm. 6% of managers said that they would take no action, and 12.5% did not know.

### **3.4 Discussion**

It is evident that PLCAs in the Western and Eastern Cape Provinces of South Africa represent a diverse industry in terms of their financial motives, adopted business models, and the efficacy of these models in meeting financial objectives. Distinct clusters of PLCAs with similar characteristics are evident, and the presence of strong negative correlations between certain characteristics suggests that incompatibilities maintain these different business models. Small PLCAs that support charismatic game (megaherbivores and large predators) can generate revenue from ecotourism but not hunting or game sales. In contrast, this incompatibility appears reduced for large PLCAs that support charismatic game. Larger PLCAs are likely to support a higher abundance of other game (bovid and equid species), allowing for multiple forms of top-down population control, such as predation, hunting and live game sales, though hunting and game sales are not intensive, comprising less than 20% of revenue. When reserves generate more than half of their revenue from hunting and game sales, large predators are absent, most likely because they would pose a financial liability by eating other valuable game. Low travel time increased the importance of day visitors, if combined with guided charismatic (“big”) game viewing opportunities. Big game reserves that charge high rates do not target local visitors or offer self-catering facilities and unguided activities, suggesting that these reserves promote a high-end experience that precludes such options. Small reserves that do not support many game species appear unable to charge high prices, which may explain why they do not offer guided activities and catering facilities that would be costly to develop and maintain. These trade-offs provide insights into why we observe current patterns of diversity in the PLCA industry, and have notable implications for profitability.

This study provides large-sample empirical support of predictions made by earlier studies that high-end guided big game ecotourism has the ability to generate greater incomes than hunting or low-end ecotourism (Barnes & de Jager 1996; Absa Group Economic Research



2003; Sims-Castley et al. 2005; Lindsey et al. 2007; Bayliss et al. 2014). While additional years of data would be useful to confirm this pattern, it is likely to be in part because big game reserves can accommodate three times more visitors than hunting reserves, and charge visitors four to six times more than budget reserves. With hunting reserves generally being high-end, low-volume and budget reserves being low-end, high volume, big game reserves appear to maximize incomes by being both high-end and high-volume.

Given the trade-offs between profitable combinations of ecology, size, accessibility, affordability, facilities and activities, two distinct business models (respectively, big game day and big game stay) emerge that display combinations of characteristics related positively with profitability. Charismatic game and guided activities are the only commonalities between these two business models. These characteristics can be combined with a small size, low travel time and the importance of day visitors; or with large size, many other game species, high price, catering facilities and the importance of international visitors.

It is important to consider not only profitability but also return on investment, which gives an indication of the efficiency of a PLCA in generating profits relative to what has been invested. Big game day reserves offer the only business model that, on average, generates returns that are comparable with the RFR (i.e. the return that could have been generated if the PLCA owner had invested the money in a minimal risk investment instead of a PLCA). The greater efficiency of big game day reserves compared with big game stay reserves is likely to be partially because big game day reserves are, on average, six times smaller and thus require fewer resources to manage (Langholz et al. 2000).

External income sources appear to play an important role in the maintenance of many PLCAs, supporting previous findings (Langholz et al. 2000; Abel et al. 2006). For owners who are not motivated to generate profits from their PLCA, particularly those that have adopted the budget business model, the sustainability of these PLCAs is likely to be dependent on the continued availability of these external income sources. Even for PLCAs currently generating a profit, their continued ability to do so is subject to the demand for game- and nature-based tourism. My findings therefore emphasize the dependence of many PLCAs on the broader-scale economic processes that drive external income generation and/or tourist demand (Abel et al. 2006).

Almost a quarter of PLCAs were not currently meeting their financial objectives. This mismatch between financial objectives and financial returns was particularly common amongst hunting reserves. With just one year of financial data, I cannot empirically assess the permanence of these mismatches or the efficacy of managers in adapting their business models

to eliminate them. As the success of a conservation organization is defined by its ability to conserve biodiversity long-term, adaptation of a PLCA's business model (e.g. changing from hunting to a big game reserve) would not represent a failure in persistence, provided that conservation objectives continue to be met. However, evidence of challenges associated with changing business models suggests that managers may not be able to readily adapt to a mismatch. Establishing a hunting reserve requires substantial sunk costs, including investment in a large land area and a high number of game species. Ecological and economic incompatibilities result in such a reserve being unable to concurrently generate substantial revenues from ecotourism, which is likely reinforced by social incompatibilities in the form of negative perceptions of many ecotourists towards hunting (McGranahan 2011). Transitioning from a hunting reserve to a big game stay reserve would require additional property investments of \$4.1 million (on average), creating a significant barrier to entry into this more profitable business model. Changing from a hunting reserve to a big game day reserve is unlikely to be successful, given that big game day reserves are characterized by high geographic accessibility, while hunting reserves are not. Furthermore, managers of hunting reserves may be unwilling to adopt guided big game ecotourism due to personal preferences and lifestyle choices (e.g. McGranahan 2011). Given the potential for these constraints to impede adaptation, it is important for us to consider the likely sustainability of mismatched PLCAs.

Owners' financial thresholds give us some indication as to whether mismatched organizations are likely to persist long-term, with over 80% of mismatched PLCAs stating that they would not continue to finance an unprofitable organization indefinitely. Over a third of managers stated that they will attempt to adapt if they do not manage to achieve the PLCAs financial objectives in the next ten years. Interestingly, while several big game reserve managers suggested closing high-end lodges and adopting hunting as a likely adaptation to a mismatch, no hunting PLCAs suggested adopting high-end ecotourism. Therefore, large-scale adaptation of multiple socioeconomic and ecological PLCA characteristics, as would be required for a PLCA to adopt a more profitable business model, appears limited on some PLCAs, in light of incompatibilities and barriers of exit and entry discussed above.

The segregation of PLCAs into distinct business models with different target markets (high-end vs. low-end, international vs. local, ecotourist vs. hunter) may reduce competition between PLCAs adopting different business models. With competition thought to be growing in the wildlife industry in southern Africa (Bond et al. 2004), mismatched PLCAs may influence competition in two notable ways. Firstly, if the managers of mismatched PLCAs

succeed in adapting to a more profitable business model, they may increase competition within this business model. Secondly, if they are unable to adapt and thereby fail, they may reduce competition within their current business model, alleviating mismatches experienced by other PLCAs within this niche. It is important, however, to note that tourists may favour spending time in areas in which they can accumulate multiple experiences and/or travel between nearby reserves. The presence of two or more nearby PLCAs may in fact increase overall visitor numbers, to the net benefit of both/all areas, creating a facilitation effect rather than a negative financial outcome. For example, during interviews with tourists undertaken as part of a related study (Ament et al. 2016), some visitors to national parks indicated that they stayed in adjacent private areas where the quality of accommodation was higher and visited the national parks during the day. This is clearly an area in which further research on synergies and tradeoffs might benefit the industry as a whole and support the achievement of conservation objectives.

The majority of PLCAs stated that nature protection was an important objective, supporting previous studies (Langholz 1996; Pasquini et al. 2010a; Selinske et al. 2015). If management attempts to increase/achieve profitability impact negatively on the PLCA's ecological integrity, attempted adaptations could lead to harmful long-term ecological effects (Langholz & Lassoie 2001; Kerley et al. 2003; Sims-Castley et al. 2005; Cousins et al. 2008), and failure to meet conservation objectives. For example, if hunting reserves were unable to meet their financial objectives, some managers reported "hunting more game" as a likely response. If increased hunting exceeds ecologically sustainable levels, this may ultimately result in game population collapses, altered food-webs, and reduced ability to persist as a conservation organization. The interdependencies between the PLCA's socioeconomic and ecological systems suggest that PLCAs are best considered as social-ecological systems (Berkes et al. 2000).

An understanding of the diversity and likely persistence of conservation organizations must incorporate the fact that organizations that govern or manage natural resources emerge from social-ecological interactions. The significance of this fact lies, in part, in the consideration of temporal scale. Socioeconomic processes like tourism demand and income can change over short time periods, while ecological processes like habitat alteration or trophic cascades generally change over much longer time scales (Cumming et al. 2015). Therefore, PLCA managers with short-term financial objectives may more readily attempt to adapt their management to socioeconomic processes than to ecological processes (Cumming et al. 2015). If these adaptations are detrimental to slower-changing ecological processes, then a temporal scale mismatch arises (Cumming et al. 2006), and the PLCA becomes gradually less resilient

to the larger shocks that may eventually emerge from ecological feedbacks (Cumming et al. 2015). The theory of structural inertia states that organizations that attempt to adapt too often and too specifically to current conditions can increase their risk of failure (Hannan & Freeman 1984). For organizations in social-ecological contexts, this hypothesis appears to fit well: I propose that there is a risk that frequent and specific adaptations in response to fast-changing socioeconomic variables can result in unforeseen but detrimental changes to slow-changing ecological variables.

### **3.5 Conclusion**

I have demonstrated that organizational ecology can be a useful framework with which to understand the likely persistence of conservation organizations. Identifying incompatibilities in organizational characteristics is useful in explaining observed diversity in conservation organizations. Through the theory of structural inertia, these incompatibilities and barriers of exit and entry can be used to explore the challenges encountered by organizations in adapting effectively to dynamic environmental conditions, such as changing recommendations regarding conservation actions and a changing economic climate (Larson et al. 2014; Armsworth et al. 2015). Conservation organizations are subject to varying degrees of financial constraint (Larson et al. 2014). “Rational routes to collapse” (Peterson et al. 2003) may arise when initial, rational choices of how to manage and conserve a natural resource in a given socioeconomic environment lead to inert organizational structures that are unable to adapt effectively to changing socioeconomic conditions. Attempted adaptations to overcome such constraints may hinder conservation efforts, and ultimately lead to organizational collapse, when socioeconomic and ecological processes operate at different temporal scales.

**Appendix 3A.** Scores of the 16 Private Land Conservation Area (PLCA) characteristics on the first two principal components (PCs) and average ( $\pm$ SE) scores for the four identified PLCA clusters (bold indicates scores  $\geq |0.5|$ ). See Table 1 for characteristic descriptions.

Characteristic	PC1	PC2
size	<b>1.07</b>	0.49
chari_game	<b>1.12</b>	<b>-0.53</b>
other_game	<b>0.95</b>	<b>0.54</b>
land_cover	0.43	-0.07
elev_var	0.27	<b>0.69</b>
travel_time	-0.06	<b>0.83</b>
price	<b>1.17</b>	0.05
bed_no	0.43	-0.38
cat.v.sc	<b>1.09</b>	-0.14
stay.v.day	0.03	<b>0.84</b>
guide.v.self	<b>0.95</b>	<b>-0.53</b>
eco	0.07	<b>-1.16</b>
hunt	-0.04	<b>1.12</b>
game_sale	0.38	<b>0.71</b>
farm	-0.48	-0.05
int.v.loc	<b>0.83</b>	0.03
Cluster	Mean PC1	Mean PC2
Hunting	0.09 $\pm$ 0.11	<b>1.07<math>\pm</math>0.10</b>
Budget	<b>-0.76<math>\pm</math>0.06</b>	-0.08 $\pm$ 0.06
Big game stay	<b>0.64<math>\pm</math>0.17</b>	0.34 $\pm$ 0.15
Big game day	0.27 $\pm$ 0.11	<b>-0.63<math>\pm</math>0.04</b>

## CHAPTER 4: POSITIVES AND PATHOLOGIES OF NATURAL RESOURCE MANAGEMENT ON PRIVATE LAND CONSERVATION AREAS

---

### Abstract

In managed natural resource systems, such as fisheries and rangelands, there is a recognized trade-off between managing for short-term benefits and managing for longer-term resilience. Management actions that stabilize ecological attributes or processes can improve productivity in the supply of ecosystem goods and services short-term, but erode system resilience at longer time scales. For example, fire suppression in rangelands can increase grass biomass short-term, but ultimately result in an undesirable, shrub-dominated system. Analyses of this phenomenon have focused largely on how management actions influence slow-changing biophysical system attributes (such as vegetation composition). Data on the frequency of management actions that reduce natural system variation on 66 Private Land Conservation Areas (PLCAs) in South Africa were used to investigate how management actions are influenced by manager decision-making approaches; a largely ignored part of the problem. The pathology of natural resource management was evident on some PLCAs: an increased focus on revenue-generation in decision-making resulted in an increased frequency of actions to stabilize short-term variation in large mammal populations, which led to increased revenues from ecotourism or hunting. On many PLCAs, these management actions corresponded with a reduced focus on ecological monitoring, and an increase in game overstocking and the number of extralimital species (occurring outside their historical range). Positives in natural resource management also existed, however, with some managers undertaking vegetation monitoring, resulting in less intensive management, lower stocking rates and fewer extralimital species. This study's unique, empirical investigation of monitoring-management relationships in natural resource management illustrates that management informed by revenue-monitoring versus ecological-monitoring can have opposing consequences for natural resource productivity and the likelihood of unsustainable management practices. Promoting management actions that maintain resilience in natural resource systems therefore requires cognizance of the ability of managers' decision-making approaches to set up either pathological or self-correcting management feedbacks.

## 4.1 Introduction

Many ecosystems and ecological processes are managed by people for the production of desirable ecosystem goods and services. Typical managed systems include such well-known examples as forests, rangelands, fisheries and agro-ecosystems. In each of these cases, there is a recognized trade-off between managing to maximize short-term benefits (often labeled as an ‘optimization’, ‘Maximum Sustainable Yield’, or ‘Command and Control’ approach) and managing for longer-term resilience (Holling & Meffe 1996). For example, the management of fisheries under a maximum sustainable yield paradigm stabilized fish harvests in the short-term, but ultimately resulted in the successive collapses of several globally important fish stocks (Larkin 1977). Other examples where the stabilization of natural system variation has ultimately resulted in disastrous ecological changes include pest control in farming monocultures, fire suppression in rangelands, and alterations to river flow regimes (Pam 1998; Folke et al. 2004). These practices are sufficiently widespread that they have been termed “the pathology of natural resource management” (Holling & Meffe 1996).

The trade-off between managing a natural system for short-term benefits and longer-term resilience can be attributed to the behaviour of system variance. Attempts to improve predictability and productivity in the supply of ecosystem goods and services through the stabilization of key ecological attributes can erode system resilience because this reduction in short-term system variance will typically increase variance at longer time scales, a phenomenon known as Bode’s law (Stein 2003). In complex systems that are subject to non-linear dynamics and multiple possible states, this increased variance can push a system over a threshold and out of its current, desirable state (Carpenter et al. 2015). Most analyses of this phenomenon have focused on the effect of management actions on biophysical variables, such as phosphorus levels in freshwater systems or shrub cover in rangelands (Wright & Heinselman 1973; Ludwig et al. 1978; Walker et al. 1981; Anderies et al. 2002; Carpenter et al. 2015).

Less attention, however, has been placed on the role of manager decision-making in driving this phenomenon. Manager decision-making is influenced by manager objectives, social norms and conservation ethics; a topic that has received considerable attention, particularly in European farming systems (Beedell & Rehman 1999; Willock et al. 1999a, 1999b; Darnhofer et al. 2005; Janssen & van Ittersum 2007; de Snoo et al. 2013; Poppenborg & Koellner 2013). Managers are therefore likely to adjust their management based on the extent to which management outcomes meet their objectives. For example, if “command and control” management actions result in short-term increases in economic productivity, managers with economic objectives can be expected to become focused on increasing efficiency in a

seemingly successful system (Holling & Meffe 1996). This means that their priorities will shift away from the “inefficient” monitoring of long, slow system attributes that are difficult and/or costly to monitor (e.g. vegetation composition in a rangeland; Anderies et al. 2002). Their focus is expected to shift instead to efficiency-associated system properties that influence resource yield and change over finer, observable scales (e.g. livestock stocking rate; Anderies et al. 2002). In the absence of broad-scale system monitoring, managers lack a way of assessing the influence of their management actions on the slow-changing variables that determine the underlying structure and thereby resilience of the system (Biggs et al. 2012). For example, in rangeland systems, management actions to enhance livestock production can ultimately influence vegetation composition, which changes over a longer time scale (Anderies et al. 2002; Seymour et al. 2010). Managers who monitor vegetation biomass and composition, and adjust fire and/or livestock management accordingly, are better able to keep their system from shifting towards an undesirable shrub-dominated state than those who do not (Anderies et al. 2002).

Commercial private land conservation areas (PLCAs) are natural resource systems with a high potential for trade-offs between management strategies motivated by economic and conservation objectives. Given their presumed conservation agenda, I would expect PLCA management approaches to reflect long-term biodiversity conservation objectives (Langholz 1996; Stolton et al. 2014; Selinske et al. 2015). They should therefore revolve around management actions that are informed by the monitoring of broad-scale system properties, and that allow for natural ecological variability (Walters & Holling 1990; Allen et al. 2011).

However, profit generation is also an important motive for the managers of many PLCAs (Langholz et al. 2000; Stolton et al. 2014), with income generation by South African PLCAs positively related to the richness of large charismatic species (Chapter 3). The need to generate an income suggests that economic objectives may give rise to management actions which reduce ecological variability in attempts to increase economic productivity (Holling & Meffe 1996). For example, the expectations of PLCA visitors may encourage managers to increase stocking levels of large mammals and thereby sightings of charismatic species (Child et al. 2013; Maciejewski & Kerley 2014b) or to improve hunting conditions through predator population control (Cousins et al. 2010). The majority of PLCAs are relatively small (<10,000 ha) and comprised of former farmland on which large mammals were extirpated (Hayward et al. 2007a). Supporting a high diversity and abundance of large mammals can therefore require intensive management in the form of game and predator reintroductions, population regulation through hunting, culling or contraception, and actions to enhance vegetation biomass and water

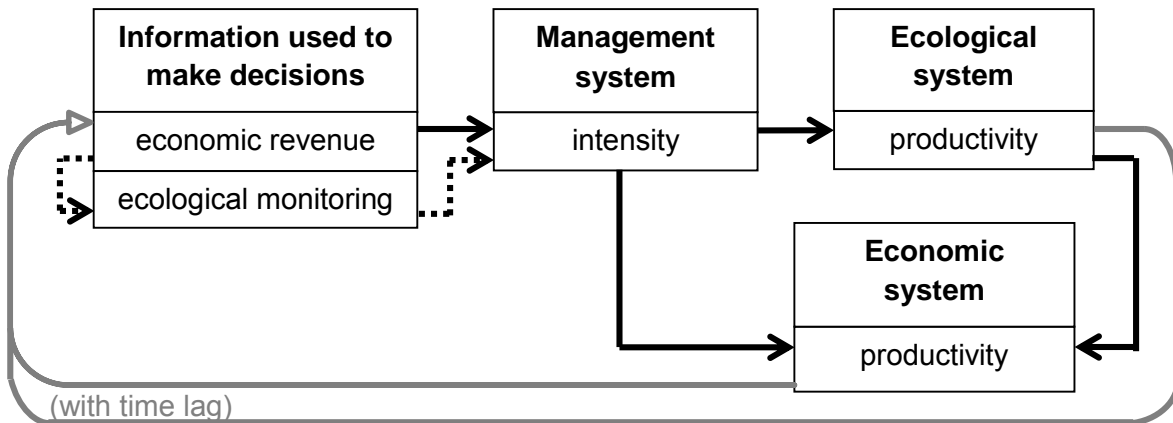


supply (Hayward et al. 2007a; Cousins et al. 2008; Child et al. 2013; Miller & Funston 2014). Bode's law suggests that stabilization of natural vegetation, water and mammal population fluctuations will increase the magnitude of these fluctuations at longer time scales, thereby eroding the resilience of the system (Stein 2003; Carpenter et al. 2015). In addition, intensive management actions and the need to sustain large populations through natural cycles of climate variation may result in an overstocking of large mammals relative to available vegetation/prey biomass, as well as the stocking of charismatic extralimital species (such as giraffe in the Eastern Cape Province, South Africa; Kettles & Slotow 2009; Cousins et al. 2010; Maciejewski & Kerley 2014a). Long-term consequences of these actions may include habitat degradation and displacement, prey population collapses, reductions in the diversity of smaller vertebrate species, and compromised genetic viability of indigenous species (Castley et al. 2001; Kettles & Slotow 2009).

In this study I undertook a novel, empirical evaluation of the interactions between manager decision-making and management actions and outcomes on PLCAs, assessing the evidence for management pathologies. I collected data on a set of closely related variables: the economic and ecological information used to inform management decisions on PLCAs, management strategies employed, ecological characteristics and economic productivity. I measured the degree of command and control management on a PLCA as the range and temporal frequency (or "intensity") of management actions that would be expected to reduce ecosystem variability (e.g. game introductions, vegetation enhancement, water provision, hunting). I quantified ecological characteristics as the richness and abundance (or "productivity") of large mammalian species (antelope, megaherbivores, large predators). I predicted that a positive relationship would exist between management intensity, ecological productivity, and short-term economic productivity (revenue generation; Fig. 1). Management intensity may influence economic productivity both directly (e.g. increased revenue from more frequent hunting) and indirectly via increased ecological productivity (e.g. increased ecotourism revenue due to higher game richness; Fig. 1).

I predicted that the more managers based their management decisions on revenue generation, the more intensively they would manage their PLCAs and the less focused they would be on monitoring slow-changing ecosystem attributes (Fig. 1). Similarly, I predicted that managers that were less focused on revenue and more focused on ecological monitoring would less intensively manage their PLCAs (Fig. 1). I used the frequency of vegetation monitoring as a proxy for the degree of focus on slow-changing attribute monitoring. Finally, I explored the potential effect of these relationships on system resilience by assessing the influence of

management intensity on the stocking of extralimital species, and the overstocking of game species. I tested my predictions using data from 66 commercial PLCAs in the Western and Eastern Cape Provinces, South Africa. PLCAs in South Africa vary widely in their management objectives and approaches (Pasquini et al. 2010a; Child et al. 2013).



**Fig. 1.** Predicted relationships between decision-making, management intensity, and ecological and economic productivity on a Private Land Conservation Area. Solid and dotted black arrows indicate positive and negative relationships, respectively, with arrow direction indicating causality. Grey arrows indicate likely feedbacks from ecological and economic system output to future decisions.

## 4.2 Methods

### 4.2.1 Decision-making: determining the information used

During interviews with the managers of 72 PLCAs in the Western and Eastern Cape Provinces of South Africa (Chapter 2), I asked managers to state how often revenue generation informed management decisions, scored from one (never) to four (always; Table 1). Managers were asked if any ecological monitoring had occurred on the PLCA. I recorded the frequency of vegetation monitoring as a score from one (never) to four (annually; Table 1), only including monitoring which had been documented (as opposed to only visually noted). 66 PLCAs provided this information.

### 4.2.2 Management system: determining management intensity

Each manager was asked to state how frequently specific management actions were undertaken (Table 1). Actions included those that “enhance” elements of the environment, such as introducing additional game (megaherbivores and antelope) or predators, providing additional food and water to improve game/predator survival, using “bomas” (enclosures < 5ha) for breeding purposes or to better monitor valuable game, and active vegetation

management, such as bush cutting and/or irrigating vegetation to enhance grass growth and thereby the biomass of grass available for large herbivores (Grossman et al. 1999; Bothma 2002). Actions that “regulate” elements of the environment included the contraception, culling, hunting or selling of game or predators. These actions were allocated an integer value for their frequency of occurrence, from one (never) to five (regularly/continuously; Table 1). The categorical frequency of 14 management actions was used to develop a composite metric for management intensity, by performing a principal component analysis (PCA; R package: *vegan*; function: *rda*; Borcard et al. 2011; Oksanen et al. 2015). Two non-trivial principal components were identified (see results) using the broken-stick method (Jackson 1993) and used to represent management intensity in subsequent analyses. Linear regressions were used to assess whether PLCA size (km<sup>2</sup>) influenced management intensity (R package: *lm*; function *stats*). Plots of fitted and observed values and residuals were examined for deviations from the assumptions of homogeneity and normality; size was log transformed to meet these assumptions. Adjusted coefficients of determination were used to assess model fit.

#### 4.2.3 *Ecological system: determining ecological productivity*

Mammal species lists from each PLCA were used to determine species richness of large predators (cheetah, brown hyaena, leopard, lion, spotted hyaena, wild dog), megaherbivores (black rhinoceros, elephant, giraffe, hippopotamus, white rhinoceros) and antelope (equid and bovid species; Table 1). Antelope, megaherbivore and predator count data were obtained from 2013 or the most recent year prior to 2013 (Table 1). Antelope, megaherbivore and predator richness and count data were scaled and used to develop a composite metric for ecological productivity, by performing a PCA. Two non-trivial principal components were identified (see results), and used to represent ecological productivity in subsequent analyses.

#### 4.2.4 *Economic system: determining economic productivity*

Ecotourism, hunting and game sale revenues generated by the PLCA during the 2013/2014 financial year were obtained for each PLCA (Table 1). Ecotourism revenue was generated from people visiting the PLCA to undertake ecotourism activities (e.g. game- and nature-viewing drives and walks; game interaction opportunities; horse riding, quad biking and off-road driving; events and functions; and environmental education/volunteering programmes), including payments for entrance, activities, food and accommodation. Hunting revenues were generated from people visiting the PLCA to hunt or observe a hunt, including payments for accommodation, hunting fees and animals hunted. Game sale revenues were

generated from the sale of venison and/or live game. Revenue figures were recorded in South African Rands, and converted to United States Dollars using the average South African Reserve Bank daily exchange rate for the 2013/2014 financial year (\$1 = R10.00).

**Table 1.** Details of management system, ecological system, economic system and decision-making information obtained for each Private Land Conservation Area. Square brackets indicate variable names referred to in the results.

Category	Details	Units of measurement
Decision-making system	[monitor_veg] vegetation monitoring	Frequency of action, allocated into categories: never (1), once (2), less than once per year (3), annually (4)
	[decision_revenue] informing management decisions based on revenue	Frequency of action, allocated into categories: never (1), occasionally (2), mostly (3), always (4)
Management system	[g_intr] game introductions	Frequency of action, allocated into categories: never (1), less than once per five years (2), less than once per year (3), a few times per year or seasonally (4), regularly/continuously (5)
	[p_intr] predator introductions	
	[g_boma] keeping game in enclosures < 5 ha	
	[p_boma] keeping predators in enclosures < 5 ha	
	[g_food] providing additional food (usually lucern) for game	
	[p_food] providing additional meat for predators	
	[water] providing man-made waterholes	
	[veg] active vegetation management to enhance grass growth	
	[g_contr] game contraception to limit reproduction	
	[p_contr] predator contraception to limit reproduction	
	[p_cull] culling predators (usually jackal and caracal)	
	[g_hunt] hunting game	
Ecological system	[g_sell] selling live game	Number
	[p_sell] selling live predators	
	[Rantelop] number (richness) of antelope species	
	[Rmega] number of megaherbivore species	
	[Rpred] number of large predator species	
	[count_antelop] abundance of antelope	
Economic system	[count_mega] abundance of megaherbivores	United States Dollars for the 2013/2014 financial year
	[count_pred] abundance of large predators	
	[rev_eco] revenue from ecotourism	
	[rev_hunt] revenue from hunting	
	[rev_game] revenue from game sales	

#### 4.2.5 *Assessing correlations between management intensity, and ecological and economic productivity*

As two principal components represented different management systems and another two represented different ecological systems (see results), I performed an exploratory PCA to assess which management and ecological systems correlated with which revenue streams (ecotourism, hunting or game sales), to inform the structural equation models described below. Revenue figures were square root transformed to satisfy the assumptions of normality, and scaled prior to performing the analysis.

#### 4.2.6 *Testing predictions using structural equation models*

To test the relationships predicted by the black arrows in Figure 1, between the management, ecological, economic and decision-making systems, I used structural equation models (SEMs). SEMs can be used to test hypotheses about causal effects through the study of path relations (Shipley 2002). They have the capacity to accommodate direct as well as indirect effects, and variables that are both responses of certain variables and predictors of others. The two identified management systems correlated uniquely with different ecological and economic systems (see results). A SEM was therefore developed for each management system, assessing the relationships between the use of economics and ecological monitoring in decision-making; and metrics representing management intensity, ecological productivity and economic productivity (R package: sem; function sem; Fox, Nie & Byrne 2012). Revenue figures were square root transformed to satisfy the assumptions of univariate as well as multivariate normality. SEMs require complete data with no missing values on any variable; 52 PLCAs provided the necessary data. Model fits were assessed using the chi-square statistic, based on the maximum likelihood method of estimation (Shipley 2002). A nonsignificant chi-square test indicates an acceptable model fit, due to a nonsignificant difference between observed and expected covariance matrices (Shipley 2002). Additional fit indices have been proposed to compensate for large sample sizes that increase power to reject models. The Bentler comparative fit index (CFI) compares the fit of the estimated model to that of a baseline or null model, which specifies that all measured variables are uncorrelated. A value of 0.95 or greater indicates a good model fit (Shipley 2002). As the models in this study fitted the data well (see results), parameter estimates were tested for significance using *z* statistics.

#### 4.2.7 *Outcomes of management strategies*

The number of nonindigenous/extralimital game species, hereafter referred to as extralimital species, was determined from national and provincial species distributions (Skinner & Chimimba 2005). Game stocking rate, as a proportion that game metabolic biomass comprised of herbivore metabolic biomass carrying capacity (*K*), was calculated for each PLCA. Game metabolic biomass (0.75 game biomass in kg/km<sup>2</sup>) was calculated (Cumming & Cumming 2003), using a “species mass” of three quarters of adult female body mass (Skinner & Chimimba 2005) in order to account for intra-species sex and age differences in biomass (Hayward & Kerley 2005). *K* (kg/km<sup>2</sup>) was determined (Coe et al. 1976; Cumming & Cumming 2003) as:

$$K = 0.02 * R^{1.69}$$

where R is average annual rainfall from 2010 to 2014, obtained from the South African Weather Services for the weather station geographically closest to each PLCA. Multiple linear regressions were used to assess whether the two identified management systems influenced (a) extralimital species richness and (b) game stocking rates (R package: stats; function: lm). Plots of fitted and observed values and residuals were examined for deviations from the assumptions of homogeneity and normality. Adjusted coefficients of determination were used to assess model fit.

Total running costs incurred by the PLCA during the 2013/2014 financial year, and those attributable to salaries and fuel specifically, were obtained for each PLCA. Costs (per square kilometre) were compared between PLCAs that annually monitored their vegetation and those that did not, using Mann-Whitney U tests due to non-normal data. Frequency of monitoring was not related to running costs using a linear model since I only had a single year of financial data, and three of the four monitoring frequencies were less than once per year (Table 1). Statistical analyses were performed in the statistical programme R (R Development Core Team 2016) at a significance level of  $\alpha = 0.05$ .

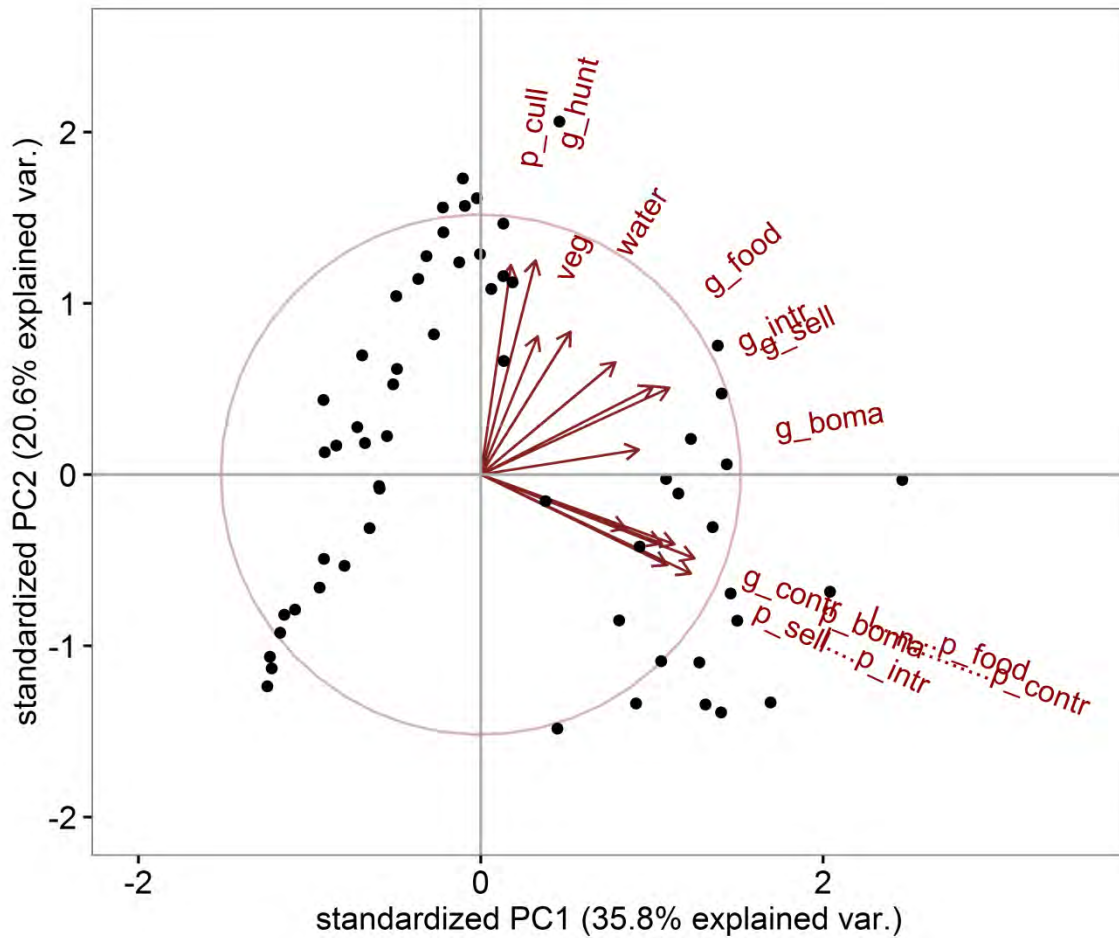
### 4.3 Results

Only 14% of PLCA managers monitored their vegetation annually; 53% never monitored their vegetation (16.5% and 16.5% monitored less than once a year and once only, respectively). In contrast, 47% of managers stated that revenue influenced all of their ecological management decisions and 16.5% stated that it never influenced their decisions (20% and 16.5% stated that revenue mostly and rarely influenced decisions, respectively).

Two principal components (PCs) accounted for 56.5% of the variation in 14 PLCA management actions and represented two unique management systems (Fig. 2). Increasing PC1 scores depicted increasing intensity of game and predator management. Higher PC1 scores corresponded with a higher frequency of management actions that enhance game and predator populations through introductions, use of bomas, provision of food and water; and management actions that regulate game and predator populations through sales and contraception (Fig. 2). This principal component is hereafter referred to as “game and predator management intensity”. Increasing PC2 scores depicted increasing intensity of game management. Higher PC2 scores corresponded with a higher frequency of management actions that enhance vegetation growth, that enhance game populations through introductions and provision of food and water, that regulate game populations through hunting and that regulate predator populations through culling (Fig. 2). The more frequently these management actions were

taken, the less frequently predators were introduced. This principal component is hereafter referred to as “game only management intensity”.

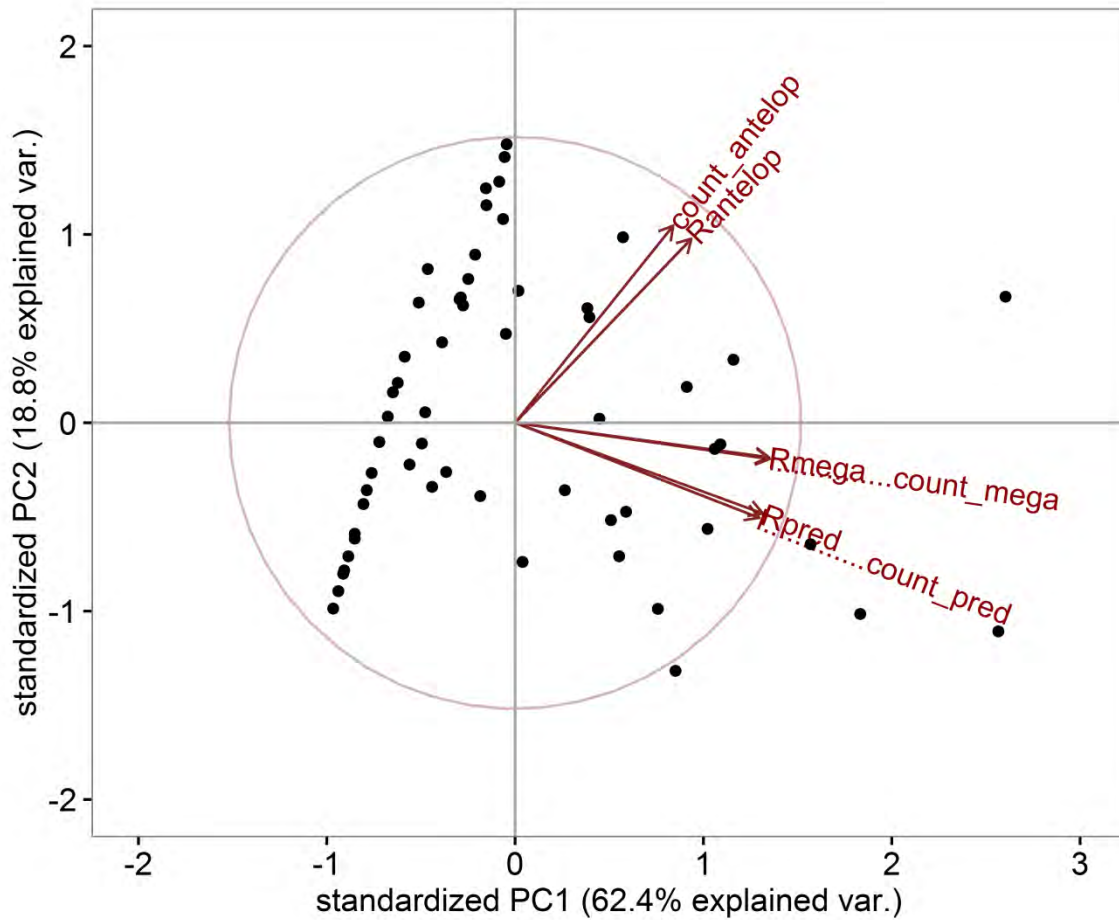
There was a weak positive relationship between PLCA size, and game and predator management intensity, with management intensity increasing with increasing PLCA size ( $r^2 = 0.20$ ;  $F = 16.79$ ,  $n = 66$ ,  $p < 0.001$ ;  $\beta = 0.43 \pm 0.1$ ,  $t = 4.10$ ,  $p < 0.001$ ). There was no relationship between PLCA size and game only management intensity ( $r^2 = 0.03$ ;  $F = 3.16$ ,  $n = 66$ ,  $p = 0.08$ ).



**Fig. 2.** Biplot depicting the relative scores of 14 Private Land Conservation Area (PLCA) management actions on two principal components (PCs). Data points indicate the scores of 66 PLCAs. See Table 1 for action descriptions and Appendix 4A for action scores on each principal component.

Two principal components accounted for 81.3% of the variation in six PLCA ecological characteristics and represented two unique ecological systems (Fig. 3). Increasing scores on PC1 depicted increasing ecological productivity in the form of antelope, megaherbivore and predator species richness and abundance (Fig. 3). This principal component is hereafter referred to as “game and predator ecological productivity”. Increasing scores on PC2 depicted

increasing ecological productivity in the form of antelope species richness and abundance only (Fig. 3). This principal component is hereafter referred to as “game ecological productivity”.



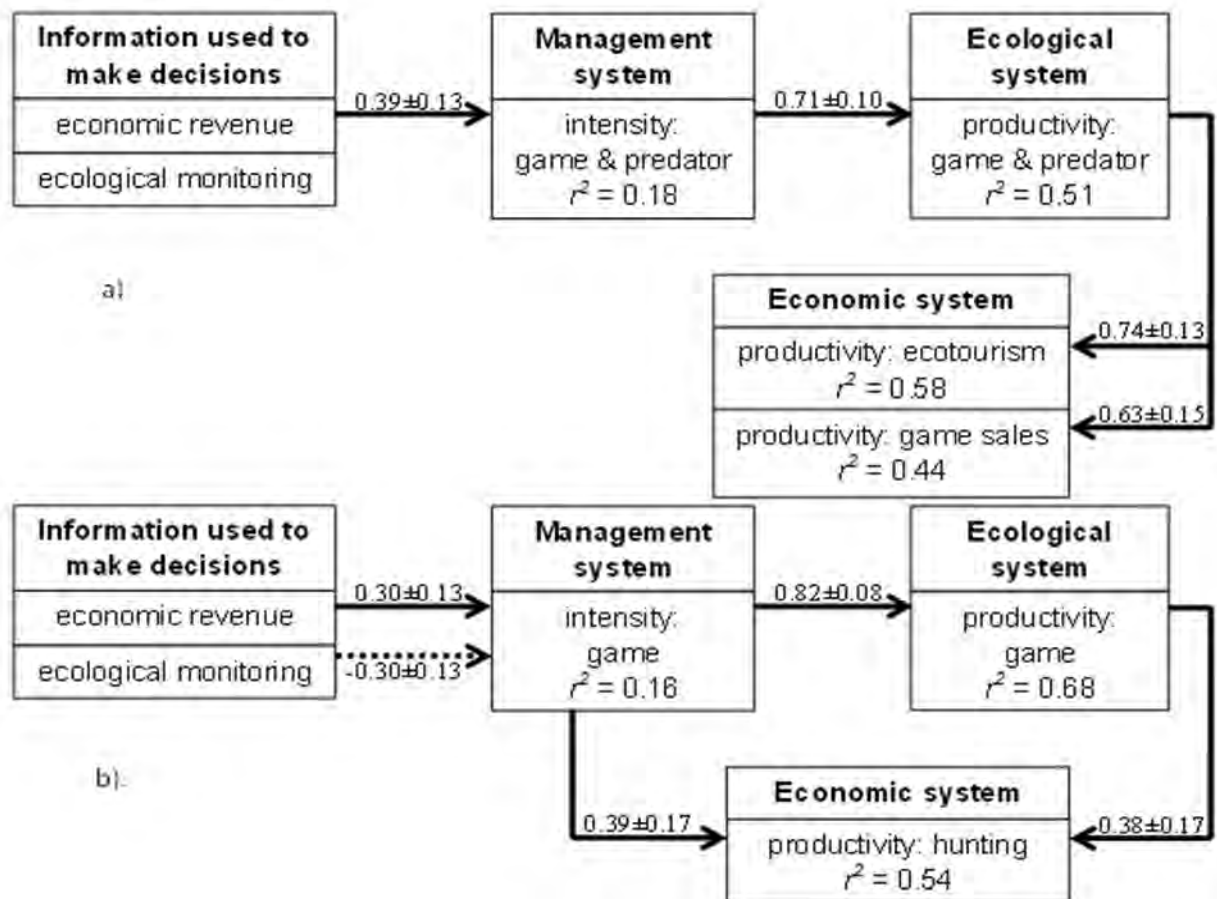
**Fig. 3.** Biplot depicting the relative scores of six Private Land Conservation Area (PLCA) ecological characteristics on two principal components (PCs). Data points indicate the scores of 66 PLCAs. See Table 1 for characteristic descriptions and Appendix 4B for characteristic scores on each principal component.

Exploratory analysis revealed positive correlations between game and predator management intensity, game and predator ecological productivity, and ecotourism and game sale revenues (Appendix 4C). Positive correlations existed between game only management intensity, game ecological productivity, and hunting revenues (Appendix 4C).

A structural equation model, using the game and predator management intensity metric, game and predator ecological productivity metric, and ecotourism and game sale revenues, fitted well the predicted relationships between decision-making, management intensity, ecological productivity and economic productivity ( $X^2 = 13.06$ , d.f. = 8,  $p = 0.1$ ;  $CFI = 0.96$ ). An increase in the use of revenue in decision-making resulted in an increase in game and



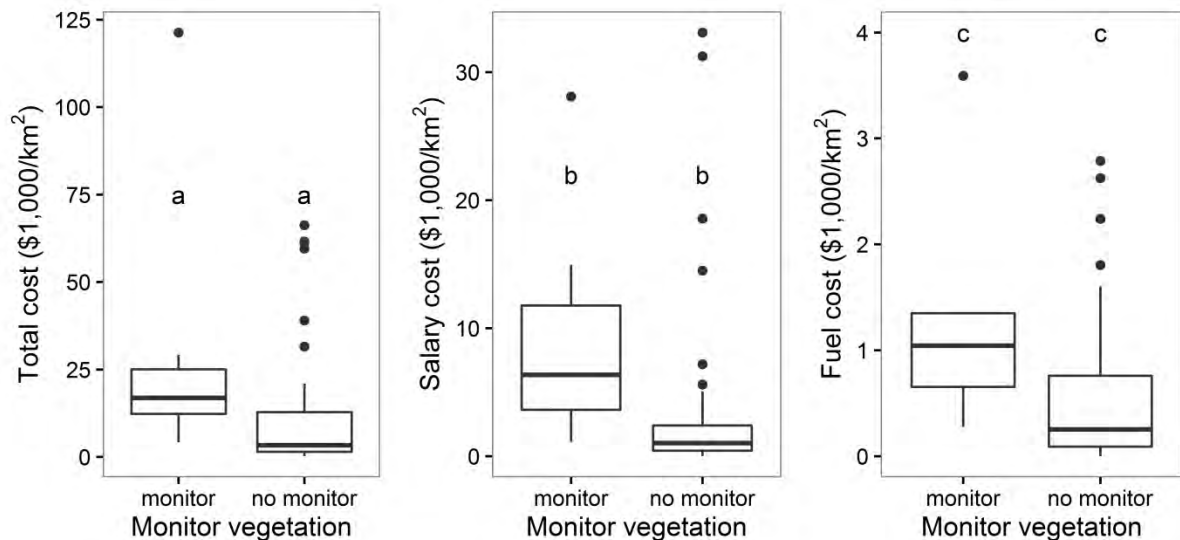
predator management intensity, which resulted in an increase in game and predator ecological productivity, which resulted in an increase in economic productivity in the form of ecotourism and game sale revenues (Fig. 4a). An increase in the use of revenue in decision-making did not influence the frequency of monitoring, and the frequency of monitoring did not influence management intensity (Appendix 4D).



**Fig. 4.** Structural equation models depicting significant relationships between the frequency of ecological monitoring and revenue use in decision-making; management intensity [(a) game and predator management intensity; (b) game only management intensity]; ecological productivity [(a) game and predator ecological productivity; (b) game only ecological productivity]; and economic productivity [(a) ecotourism and game sales revenues; (b) hunting revenues]. Coefficients of determination ( $r^2$ ) indicate the proportion of variance of a variable explained by all predictor variables. Solid and dotted black arrows indicate statistically significant positive and negative relationships, respectively, with arrow direction indicating causality and the values above each arrow indicating the standardized effect ( $\pm$ SE). Refer to Appendix 4D for complete statistical output.

A structural equation model using the game only management intensity metric, game ecological productivity metric, and hunting revenue, was found to be a good fit of the predicted relationships between decision-making, management intensity, ecological productivity and economic productivity ( $X^2 = 3.15$ , d.f. = 5,  $p = 0.7$ ;  $CFI > 0.99$ ). An increase in the use of revenue in decision-making resulted in an increase in game management intensity, which resulted in an increase in economic productivity in the form of hunting revenues, both directly and indirectly via increased game ecological productivity (Fig. 4b). An increase in the use of revenue in decision-making did not influence the frequency of monitoring; the frequency of monitoring negatively influenced game management intensity (Fig. 4b; Appendix 4D).

The richness of extralimital species increased significantly with increases in game and predator management intensity, and game only management intensity ( $r^2 = 0.44$ ,  $F = 20.95$ ,  $n = 52$ ,  $p < 0.001$ ;  $\beta_{game\&pred} = 1.20 \pm 0.40$ ,  $t = 3.04$ ,  $p = 0.004$ ;  $\beta_{game} = 2.10 \pm 0.39$ ,  $t = 5.42$ ,  $p < 0.001$ ). Game stocking rate, relative to game carrying capacity, increased significantly with game only management intensity, while game and predator management intensity did not influence game stocking rate ( $r^2 = 0.30$ ,  $F = 11.96$ ,  $n = 52$ ,  $p < 0.001$ ;  $\beta_{game} = 0.85 \pm 0.19$ ,  $t = 4.57$ ,  $p < 0.001$ ;  $\beta_{game\&pred} = 0.25 \pm 0.19$ ,  $t = 1.33$ ,  $p = 0.19$ ). PLCAs that regularly monitored their vegetation had significantly higher running costs per square kilometre than those that did not, spending significantly more money on salaries and fuel (Fig. 5).



**Fig. 5.** Running costs incurred by Private Land Conservation Areas that regularly monitored their vegetation, compared with those that did not. (Letters indicate significant difference: a.  $W = 70$ ,  $p = 0.004$ ; b.  $W = 54$ ,  $p = 0.002$ ; c.  $W = 34$ ,  $p = 0.03$ ).

#### 4.4 Discussion

My analyses show that the economic productivity of managed natural resources on a PLCA is closely related to the regulation of short-term variation in those resources. The more intensive the management of large mammal populations, the greater their richness and abundance, and the greater the revenues generated from them. It is important to note that this trend is likely to be short-term and only up to a point; for example, above a threshold elephant density, increased elephant densities do not attract more tourists or increase sighting success rates (Maciejewski & Kerley 2014b). The intensity of large mammal population management corresponded with the degree to which revenue generation influenced management decisions. I therefore found evidence that the natural resource management pathology occurs on South African PLCAs: the more focused managers are on generating revenue, the more they undertake command and control management actions and the more productive (in the short-term and up to a limit) their managed systems become. With attention focused predominantly on optimizing and stabilizing fast-changing variables (such as revenue, large mammal richness and abundance), slower-changing variables such as vegetation composition are generally overlooked, with over half of PLCA managers never monitoring their vegetation and just 14% monitoring it regularly.

Contrary to predictions, managers that were less focused on revenue generation were not more likely to monitor slow-changing system variables (vegetation). While many PLCA owners are motivated by objectives other than profit, such as lifestyle or philanthropy, the lack of governmental funding to PLCAs globally means that owners are responsible for the funds required to sustain their PLCAs, regardless of their motivations (Langholz 1996; Langholz & Lassoie 2001; Kabii & Horwitz 2006; Stolton et al. 2014; Selinske et al. 2015). Vegetation monitoring is costly, associated with increased salary and fuel costs, perhaps because specialized staff and sufficient resources are necessary to implement monitoring (McDonald-Madden et al. 2010). It is therefore possible that monitoring is prohibitively expensive on many of the PLCAs that do not undertake the command and control actions shown to increase revenue.

I do not have a direct means of assessing the influence of management strategies on slow-changing system variables, such as vegetation composition, and thereby their consequences for system resilience. I infer these potential consequences by considering the influence of management intensity on the richness of extralimital species, and the stocking rates of game species. The more intensively a PLCA was managed, the higher the richness of extralimital species. These species are often introduced because they are desirable to

ecotourists or hunters, but have negative effects on the vegetation, as well as indigenous mammals (Castley et al. 2001; Cousins et al. 2008; Maciejewski & Kerley 2014a). Similarly, the more intensively game on a PLCA was managed (in the absence of predators), the higher the game stocking rate, relative to that which can be sustained on available vegetation biomass. My estimates suggest that just over a quarter of PLCAs were overstocked by more than 50%, suggesting that intensive game management can lead to unsustainable pressures on the vegetation.

The negative relationship between the frequency of vegetation monitoring and game management intensity suggests that a self-correcting feedback can take effect on PLCAs that frequently monitor their vegetation. Managers that monitor their vegetation are more likely to observe the detrimental effects of game overstocking and extralimital species on the vegetation, and respond by reducing the intensity of actions that gave rise to this problem. Hence we observe a reduction in management intensity following an increase in monitoring. Interestingly, we do not observe this relationship between management intensity and monitoring on PLCAs that support both game and predators. There is no relationship between management intensity and game stocking rate on PLCAs that have introduced predators, likely because predation regulates game abundance (Hunter 1998; Power 2003; Tambling & du Toit 2005; Miller et al. 2013). It is therefore logical that vegetation monitoring does not result in the decision to reduce management intensity on these PLCAs. On the contrary, given signs of overgrazing, it may be necessary to increase the intensity of predator management in order to encourage game population regulation by predators. There is however, a concern that the high predator abundances which result from intensive management may have a detrimental impact on smaller mammal species, which are not usually managed or monitored (see Chapter 5; Harrington et al. 1999; Hayward 2011). While this study only considered vegetation monitoring, it would be interesting to explore the frequency of monitoring small “non-charismatic” mammal species. I would predict that on PLCAs supporting large predators, managers that frequently monitored their small mammal communities would undertake less intensive predator management (resulting in lower predator abundances) than those who were focused primarily on revenue generation and did not undertake ecological monitoring.

It is interesting that the two observed management systems influenced natural resource productivity in different ways. If a manager introduced and intensively managed game only, then the PLCA generated revenue from hunting. In contrast, if the manager introduced and intensively managed game and predators, then the PLCA generated revenue from ecotourism and, to a lesser extent, game sales. Large, charismatic mammals rank highest in the preferences

of visitors to protected areas in South Africa (Lindsey et al. 2007; Di Minin et al. 2013; Maciejewski & Kerley 2014a), and PLCAs supporting megaherbivores and large predators generate the greatest incomes, predominantly from ecotourism (Chapter 3). While these PLCAs can undertake hunting and game sales to some extent, dependent on their size, a focus on hunting necessitates the removal of predators, which kill valuable antelope species (Chapter 3; Cousins et al. 2008).

It has been suggested that smaller reserves require more intensive management (Hayward et al. 2007a; Funston 2008; Miller et al. 2013), and it is therefore surprising that we do not observe a reduction in management intensity with increasing PLCA size. The average size of PLCAs in this study was just 5,400 ha, in comparison to the 1,948,500 ha Kruger National Park that is given as an example of a large reserve in need of less intensive management (Funston 2008). It is therefore possible that no PLCAs in this study were large enough to facilitate natural ecological processes in the absence of management. Conservancies (the merging of multiple properties) are considered a useful tool in increasing the size of a given conservation area, and would likely play an important role in enabling a reduction in the intensive management practices currently observed on some PLCAs (Lindsey et al. 2009).

Models have been used to assess the biophysical implications of managing short-term variation in natural resource systems (Walker et al. 1981; Anderies et al. 2002; Carpenter et al. 2015). Models have further shown that management-monitoring feedbacks can improve the sustainability of resource management in uncertain environments, but lead to “rational routes to collapse” when management decisions are informed by short-term ecosystem trends and decision support tools cannot consider past trends or system thresholds (Peterson et al. 2003; Lindkvist & Norberg 2014). My study builds on these model predictions by showing *empirically* that monitoring-management relationships exist in natural resource management, and that management informed by revenue-monitoring versus ecological-monitoring can have opposing consequences for natural resource productivity and the likelihood of unsustainable management practices. Amongst other things, this finding has some important implications for our understanding of the relationships between revenue generation and tourism. Tourists may be unaware that the pressure they exert on managers can lead to management practices that are detrimental to conservation objectives. As I have shown, empirical data can be used to explore and better understand the relationships between decision-making, strategies for generating revenue, and economic productivity in natural resource management.

## **4.5 Conclusion**

Even in natural resource systems with long-term conservation objectives, managers can find themselves focusing on productivity; reducing variance in fast-changing system attributes when the sustainability of a system is dependent on its economic viability. If they are continually responding to changes in revenue generation that can be detected over a shorter time scale than the ecological variation that ultimately determines system resilience, managers can slip into less sustainable management regimes despite their conservation objectives. Therefore, in addition to building recommendations for how natural resources should be managed (Carpenter et al. 2015), an important, yet largely ignored aspect of promoting resilient natural resource systems entails understanding why managers act as they do and how, why, and when their actions may drift towards unsustainability.

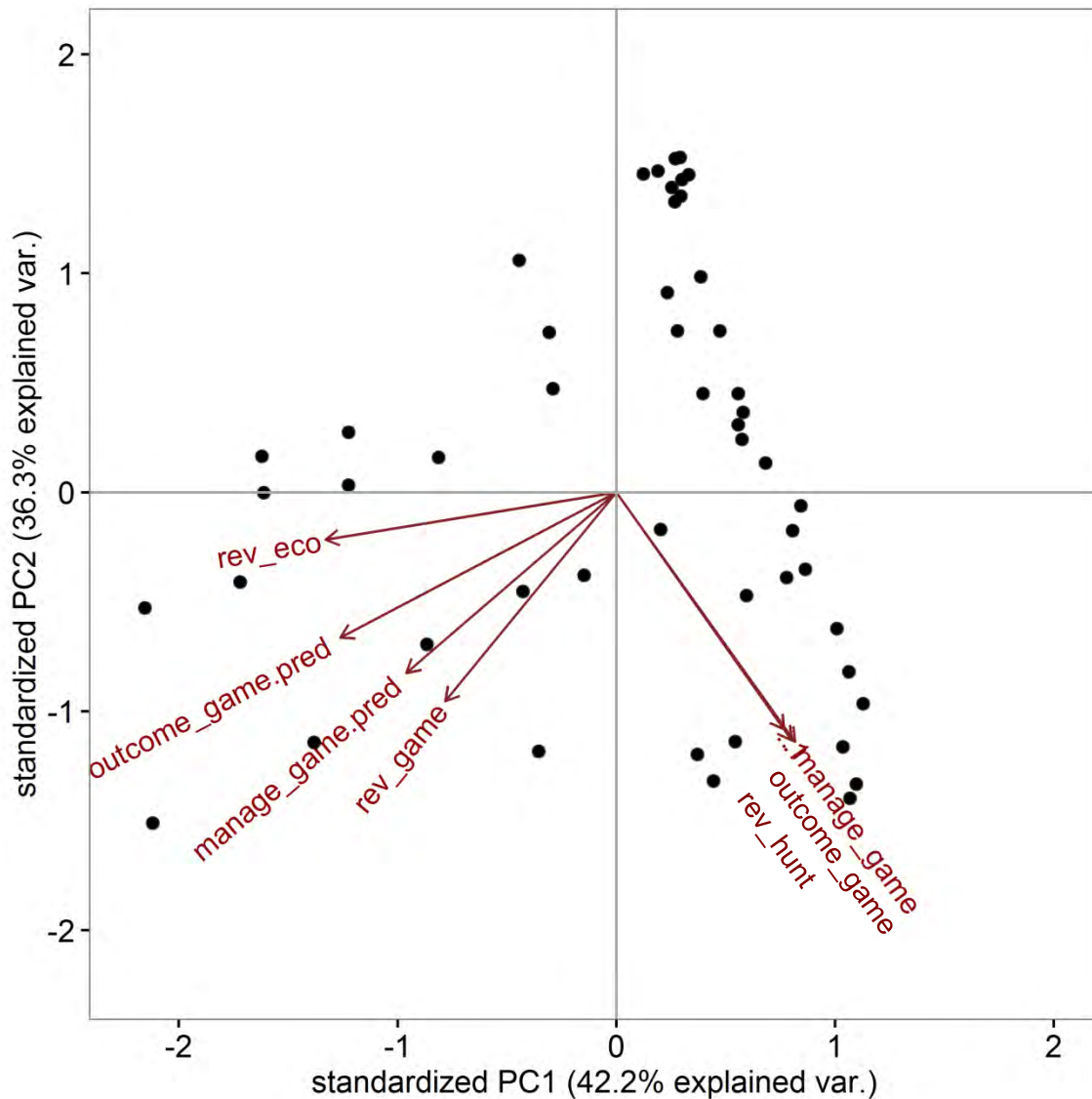
**Appendix 4A.** Scores of 14 Private Land Conservation Area management actions on the first two principal components (bold indicates scores  $\geq |0.5|$ ).

Action	PC1	PC2
veg	0.32	<b>0.78</b>
water	<b>0.51</b>	<b>0.81</b>
g_intr	<b>0.97</b>	<b>0.50</b>
g_food	<b>0.76</b>	<b>0.63</b>
g_boma	<b>0.89</b>	0.14
g_sell	<b>1.06</b>	0.49
g_hunt	0.31	<b>1.21</b>
g_contr	<b>0.82</b>	-0.30
p_intr	<b>1.19</b>	<b>-0.56</b>
p_food	<b>1.09</b>	-0.39
p_boma	<b>1.21</b>	-0.47
p_sell	<b>1.05</b>	<b>-0.51</b>
p_cull	0.17	<b>1.18</b>
p_contr	<b>1.02</b>	-0.39

**Appendix 4B.** Scores of six Private Land Conservation Area ecological characteristics on the first two principal components (bold indicates scores  $\geq |0.5|$ ).

Characteristic	PC1	PC2
count_game	<b>1.00</b>	<b>1.25</b>
count_mega	<b>1.61</b>	-0.23
count_pred	<b>1.55</b>	<b>-0.60</b>
Rantelop	<b>1.12</b>	<b>1.17</b>
Rmega	<b>1.61</b>	-0.22
Rpred	<b>1.57</b>	<b>-0.57</b>

**Appendix 4C.** Biplot of two principal component (PC) axes depicting correlations between Private Land Conservation Area (PLCA) management intensity, ecological productivity and economic productivity. (rev\_eco: ecotourism revenue; outcome\_game.pred: game and predator ecological productivity; manage\_game.pred: game and predator management intensity; rev\_game: game sale revenue; manage\_game: game only management intensity; outcome\_game: game ecological productivity; rev\_hunt: hunting revenue). Data points indicate scores of 52 PLCAs.





**Appendix 4D.** Results of two Structural Equation Models, depicting coefficients and significance of relationships between management intensity, ecological and economic productivity and decision-making variables. Arrows indicate causality; double-headed arrows indicate estimates of error for response variables.

Relationship	Coefficient	Coefficient SE	z	p
MODEL 1:				
decision_revenue -> manage_game.pred	0.39	0.13	2.95	0.003*
decision_revenue -> monitor_veg	0.11	0.14	0.80	0.43
monitor_veg -> manage_game.pred	0.13	0.13	0.96	0.34
manage_game.pred -> outcome_game.pred	0.71	0.10	7.13	<0.001*
manage_game.pred -> rev_eco	0.03	0.13	0.24	0.81
manage_game.pred -> rev_game	0.04	0.15	0.27	0.79
outcome_game.pred -> rev_eco	0.74	0.13	5.54	<0.001*
outcome_game.pred -> rev_game	0.63	0.15	4.12	<0.001*
manage_game.pred <--> manage_game.pred	0.83	0.17	4.95	<0.001*
monitor_veg <--> monitor_veg	0.99	0.20	4.95	<0.001*
outcome_game.pred <--> outcome_game.pred	0.49	0.10	4.95	<0.001*
rev_eco <--> rev_eco	0.42	0.09	4.95	<0.001*
rev_game <--> rev_game	0.56	0.11	4.95	<0.001*
MODEL 2:				
decision_revenue -> manage_game	0.30	0.13	2.31	0.02*
decision_revenue -> monitor_veg	0.11	0.14	0.80	0.43
monitor_veg -> manage_game	-0.30	0.13	-2.30	0.02*
manage_game -> outcome_game	0.82	0.08	10.17	<0.001*
manage_game -> rev_hunt	0.39	0.17	2.28	0.02*
outcome_game -> rev_hunt	0.38	0.17	2.21	0.03*
manage_game <--> manage_game	0.84	0.17	4.95	<0.001*
monitor_veg <--> monitor_veg	0.99	0.20	4.95	<0.001*
outcome_game <--> outcome_game	0.32	0.06	4.95	<0.001*
rev_hunt <--> rev_hunt	0.46	0.09	4.95	<0.001*

NOTE: manage\_game.pred: game and predator management intensity; manage\_game: game only management intensity; outcome\_game.pred: game and predator ecological productivity; outcome\_game: game ecological productivity; rev\_eco: ecotourism revenue; rev\_game: game sale revenue; rev\_hunt: hunting revenue; decision\_revenue: frequency of management decisions informed by revenue; monitor\_veg: frequency of vegetation monitoring; SE: standard error; \*significant)

## **CHAPTER 5: PREDATORS ON PRIVATE LAND: BROAD-SCALE SOCIOECONOMIC INTERACTIONS INFLUENCE LARGE PREDATOR MANAGEMENT**

---

### **Abstract**

The proliferation of private land conservation areas (PLCAs) is placing increasing pressure on conservation authorities to effectively regulate their ecological management. Many PLCAs depend on tourism for income, and charismatic large mammal species are considered important for attracting international visitors. Broad-scale socioeconomic factors therefore have the potential to drive fine-scale ecological management, creating a systemic scale mismatch that can reduce long-term sustainability in cases where economic and conservation objectives are not perfectly aligned. I assessed the socioeconomic drivers and outcomes of large predator management on PLCAs in South Africa. Managers of PLCAs stocking free-roaming large predators identified revenue generation as influencing most or all of their management decisions and rated profit generation as a more important objective than did the managers of PLCAs that did not stock large predators. Ecotourism revenue increased with increasing lion density, creating a potential economic incentive for stocking lion at high densities. Despite this potential mismatch between economic and ecological objectives, lion densities were sustainable relative to available prey. Regional-scale policy guidelines for free-roaming lion management were ecologically sound. By contrast, policy guidelines underestimated the area required to sustain cheetah, which occurred at unsustainable densities relative to available prey. Evidence of predator overstocking included predator diet supplementation and frequent reintroduction of game. I conclude that effective facilitation of conservation on private land requires consideration of the strong and not necessarily beneficial multi-scale socioeconomic factors that influence private land management.

### **5.1 Introduction**

Many of the challenges encountered by societies in managing natural resources arise because of a mismatch between the scale of management and the scale of ecological processes being managed (Cumming et al. 2006). For example, in the absence of regional and global institutions with the power to regulate fishing harvests at spatial and temporal scales appropriate for (often poorly understood) fish population dynamics, societies have overexploited fish populations (Hilborn et al. 2005). Mitigating such challenges requires an

understanding of the multi-scale processes that influence management and the development of approaches for realigning socioeconomic and ecological system elements.

Protected areas represent a key strategy for biodiversity conservation globally, but their effectiveness depends on appropriate management of the ecological patterns and processes within their boundaries (Chape et al. 2005). Protected area management is influenced by social-ecological elements that interact over diverse spatial and temporal scales and institutional levels; from patch-level ecosystem patterns and processes to national land tenure policies and global economies that influence tourism and other economic opportunities (Cumming et al. 2015). Scale mismatches can hinder the conservation effectiveness of protected areas when differences between the scale of ecosystem processes and the scale of institutions relating to ecosystem management result in ecological process disruptions and/or biodiversity losses (Maciejewski et al. 2015). For example, size limitations of fenced protected areas impede the natural large-scale movements of elephant, with associated increases in elephant densities impacting negatively on other biodiversity within these areas (Cumming et al. 1997; Kerley & Landman 2006).

With state-owned protected areas proving to be insufficient to meet biodiversity conservation targets (Jenkins & Joppa 2009; Watson et al. 2014), private landowners have become important role players in conserving and connecting biodiversity globally (Fitzsimons & Wescott 2008; Gallo et al. 2009; Stolton et al. 2014). Despite their importance for biodiversity conservation, there are concerns that unsustainable ecological management on some private land conservation areas (PLCAs) will undermine their long-term conservation objectives. Firstly, PLCAs often comprise relatively small tracts of land (< 10,000 ha); there are concerns that many PLCAs in southern African and Latin America are too small to effectively conserve species with large spatial requirements, such as megaherbivores and large predators (Creel et al. 2013; Miller & Funston 2014; Pegas & Castley 2016). Secondly, the financial objectives of many commercial PLCAs and their reliance on revenue-generating activities may result in ecological management decisions that are heavily influenced by the expectations of paying visitors (Langholz & Lassoie 2001; Cousins et al. 2010; Miller et al. 2013; Maciejewski & Kerley 2014a). The financial objectives of a PLCA influence the business model that is adopted (Chapter 3). This includes how many large mammal (megaherbivore and large predator) species are introduced, with PLCA revenue positively related to the abundance of large mammal species (Chapter 4). The perception that visitors demand high quality animal sightings may lead to unsustainable stocking rates of these charismatic species in order to improve tourist satisfaction and thereby generate revenue

(Lindsey et al. 2007; Kettles & Slotow 2009; Maciejewski & Kerley 2014b). Conservation authorities have the ability to mitigate these concerns by way of policy. For example, in order to introduce “dangerous game” (megaherbivores and large predators) onto a PLCA in South Africa, the landowner is required to obtain a Certificate of Adequate Enclosure by fulfilling requirements outlined in the relevant provincial (i.e. regional) policy (e.g. Department of Economic Development and Environmental Affairs 2008).

The potential interactions between manager objectives, land size, policy, tourist demands and large mammal management are multi-scale. A manager with a given land area may reintroduce charismatic large mammal species (ecological elements at the PLCA scale) as a result of his/her financial objectives (socioeconomic elements at the PLCA scale) and the perceived demand from tourists (socioeconomic elements at the national and international scale; Fig. 1; Maciejewski et al. 2015). Stocked mammals thereafter impact on other patch- and PLCA-scale ecological elements, through habitat and/or prey preferences (Fig. 1), resulting in potentially deleterious ecological effects if these species are overstocked relative to resource availability (Kerley & Landman 2006; Kettles & Slotow 2009). Regional-scale policy may prevent PLCA-scale overstocking, provided policy requirements are ecologically meaningful, and enforced (Fig. 1).

To explore the relevance of multi-scale socioeconomic factors for the management of PLCAs, I focused on PLCAs that stock large predators (cheetah, lion, spotted hyaena, and wild dog) in the Eastern and Western Cape Provinces of South Africa. Applying the concept of scale mismatches, I predicted that unsustainable stocking densities of large predators might arise if (1) policy guidelines relating to predator management are inappropriate, and/or (2) PLCA managers express financial objectives and ecotourism revenue is higher at higher densities of large predators.

Ecological units	Scale	Institutional/social units
	International International institutional context	International tourists
Network of PLCAs between which large mammals are translocated	National National institutional context	National tourists
Network of PLCAs between which large mammals are translocated	Regional/provincial Proximate institutional context	Provincial government policies regarding stocking large mammals
Large mammal stocking densities within a fenced area	PLCA Single tenure unit	PLCA owner and manager objectives, PLCA revenue derived from ecotourism
Large mammal habitat and/or prey preferences; habitat and prey composition and distribution	Patch Sub-tenure unit	PLCA management actions regarding large mammals (e.g., water provision, population control)

**Fig. 1.** Summary of multiscale socioecological patterns and processes related to large charismatic mammal management on Private Land Conservation Areas (PLCAs), based on the protected area framework presented in (Cumming et al. 2015) and (Maciejewski et al. 2015). Each unit represents both a spatial scale (akin to traditional ecological spatial scales; Poiani et al. 2000) and an institutional level.

## 5.2 Methods

### 5.2.1 *Determining predator presence and observed predator densities*

During interviews with the managers of 72 PLCAs in the Western and Eastern Cape Provinces of South Africa (Chapter 2), I asked managers to state which (if any) large predator species (cheetah, lion, spotted hyaena, wild dog) had been reintroduced onto the PLCA. Leopard were excluded from this list because they are not constrained by fences, have vast home ranges that span multiple properties, and their secretive nature means that they are rarely seen by tourists (Hayward et al. 2007b; Fattebert et al. 2015). Spotted hyaena and wild dog occurred on one and no PLCAs, respectively (see results), and were therefore excluded from further analyses. Managers were asked whether predators had access to the entire PLCA or were maintained within a subsection of the PLCA. Free-roaming lion and cheetah were defined

as those occurring on a minimum area of 2,000 ha or 1,000 ha, respectively (see section 5.2.5). Predators occurring in areas less than this are hereafter referred to as “captive” predators. The population size and density of each free-roaming large predator species occurring on each PLCA in 2013 was recorded. If the predator(s) occurred on a subsection of a PLCA, the area of this section was used to determine density. These predator densities are hereafter referred to as “observed predator densities”.

### 5.2.2 *Assessing the influence of managers’ financial objectives on predator management*

Managers were asked to rate profit generation as an objective, on a Likert scale from one (not important) to five (very important). Ratings from PLCAs that stocked free-roaming predators (“predator-present PLCAs”) were compared to those from PLCAs that did not stock predators (neither free-roaming nor captive; “predator-absent PLCAs”), using a Mann-Whitney U test due to non-normal data. Managers of PLCAs that stocked free-roaming predators were further asked to state how often revenue generation informed their management decisions, and answers were allocated a frequency category: never, occasionally, mostly or always.

### 5.2.3 *Assessing the influence of predator management on ecotourism revenue*

Total ecotourism revenue generated during the 2013/2014 financial year was obtained for 11 predator-present PLCAs and 37 predator-absent PLCAs. Ecotourism revenue included payments for entrance, food, accommodation and activities. Activities included game- and nature-viewing drives and walks, game interaction opportunities, horse riding, quad biking and off-road driving, events and functions, and environmental programmes. Ecotourism revenue was recorded in South African Rands, and converted to United States Dollars using the average South African Reserve Bank daily exchange rate for the 2013/2014 financial year (\$1 = R10.00). Ecotourism revenue was compared between predator-present and predator-absent PLCAs using a Mann-Whitney U test due to non-normal data.

On predator-present PLCAs for which both predator density and ecotourism revenue were available ( $n = 10$ ), I used linear regressions to assess whether (a) observed lion density and (b) observed cheetah density were significant predictors of ecotourism revenue (R package: stats; function: lm). Plots of fitted and observed values and residuals were examined for deviations from the assumptions of homogeneity and normality. Ecotourism revenue was square root transformed in order to meet these assumptions. Adjusted coefficients of determination were used to assess model fit.

#### 5.2.4 *Determining sustainable predator densities*

Ungulate count data were obtained, from 2013 or the most recent year prior to 2013, from predator-present PLCAs. Ungulates that are difficult to count due to their habitat preferences, solitary nature and/or small size (common duiker, grysbok *Raphicerus melanotis*, klipspringer *Oreotragus oreotragus*, steenbok), and thereby absent in many PLCAs' count data, were excluded. If predators occurred on a subsection of a PLCA, ungulate count data for that subsection were obtained.

The biomass ( $\text{kg}/\text{km}^2$ ) of the lion's preferred prey species has been shown to be a significant predictor of lion density, and the biomass ( $\text{kg}/\text{km}^2$ ) of prey in the cheetah's preferred prey weight range has been shown to be a significant predictor of cheetah density (Hayward et al. 2007c). These relationships can be used to determine the density of predators that a given prey population can sustain (Hayward et al. 2007c). This density is hereafter referred to as the "sustainable predator density". I used PLCA ungulate count data to determine the biomass ( $\text{kg}/\text{km}^2$ ) of preferred prey species of lion and the biomass ( $\text{kg}/\text{km}^2$ ) of prey species in the preferred weight range of cheetah on each PLCA that stocked these predators (Hayward et al. 2007c). Three quarters of the adult female body mass was used (to account for differences in mass between male, female and juvenile prey individuals; Skinner & Chimimba 2005; Hayward et al. 2007c). Ungulate count data were not corrected for visibility, as predator prey preferences and density equations were developed using uncorrected data (Hayward et al. 2007c) and correcting data would result in overestimations of sustainable predator densities. None of the ungulate species that were excluded from count data fall within the preference categories of either predator (Hayward et al. 2007c).

#### 5.2.5 *Comparing sustainable predator densities with policy guidelines*

In the Eastern Cape Province, the Certificate of Adequate Enclosure and Dangerous Game Fencing Specifications Policy (Department of Economic Development and Environmental Affairs 2008) states that, together with compiling a management plan and meeting fencing specifications, "the recommended minimum area to introduce dangerous game is 2000 ha depending on topography, habitat, prey availability and carrying capacity. (Hippopotamus and cheetah are excluded from the minimum of 2000 ha and require 1000 ha depending on habitat and topography)". The Policy on Fencing and Enclosure of Game, Predators and Dangerous Animals in the Western Cape Province (Cape Nature Biodiversity Support Services 2014) provides no guidelines for minimum area requirements of "free-roaming" predators, but states that the required management plan should include "the

maximum capacity per species provided for at the facility”. For PLCAs that stocked lion, I used the sustainable lion densities estimated above to determine the number of lion that could be sustainably supported on the specified minimum required area of 2,000 ha. Similarly, the number of cheetah that could be sustainably supported on the specified minimum required area of 1,000 ha was determined for each PLCA that stocked cheetah.

#### 5.2.6 *Assessing the sustainability of predator management*

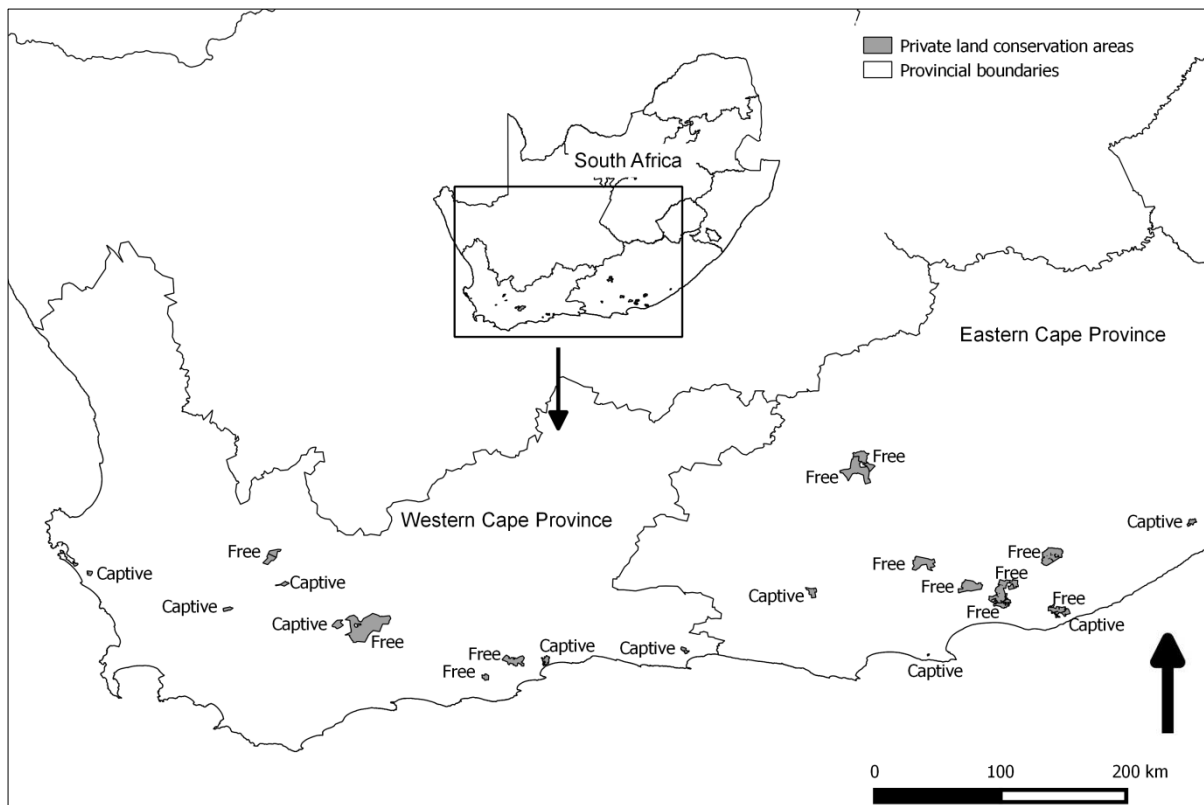
I assessed whether PLCAs were over- or under-stocking their PLCAs relative to sustainable predator densities. For each predator-present PLCA, I compared the observed density of each predator species with the sustainable density, using a paired sample t-test where data met the assumption of normality, and a paired Wilcoxon signed-rank test where data did not. Stocking densities at individual PLCAs were considered unsustainable if they exceeded sustainable density estimates by more than 5%. Managers were asked whether they made use of predator contraception, sold/relocated predators and/or supplemented predator diet on a regular basis, as well as whether they introduced additional game at least once every five years. I determined the proportion of managers undertaking these actions on PLCAs where all predator species were sustainably stocked, and those where at least one species was unsustainably stocked. Statistical analyses were performed in the statistical programme R (R Development Core Team 2016) at a significance level of  $\alpha = 0.05$ .

### 5.3 Results

Of the 72 PLCAs sampled, 22 stocked at least one large predator species (Fig. 2). On average, these 22 PLCAs stocked two ( $1.8 \pm 0.1$ ) large predator species, with a maximum of three species. Ten PLCAs supported all predators in “captivity” (i.e. within an area  $< 2,000$  ha or  $< 1,000$  ha for cheetah), and twelve PLCAs supported “free-roaming” predators (i.e. within an area  $> 2,000$  ha or  $> 1,000$  ha for cheetah). Free-roaming predators occurred on land areas ranging from 2,300 ha to 54,400 ha (mean =  $14,600 \pm 4,000$  ha).

Free-roaming cheetah and lion co-occurred on five PLCAs (Appendix 5A). Cheetah occurred as the sole predator on four PLCAs (Appendix 5A). Lion co-occurred with spotted hyaena on one PLCA and as the sole predator on two PLCAs (Appendix 5A). Average population sizes were  $5 \pm 1$  cheetah and  $8 \pm 2$  lion, average densities were  $0.05 \pm 0.02$  cheetah/km<sup>2</sup> and  $0.05 \pm 0.01$  lion/km<sup>2</sup> (Appendix 5A). Wild dog were not present on any PLCAs.

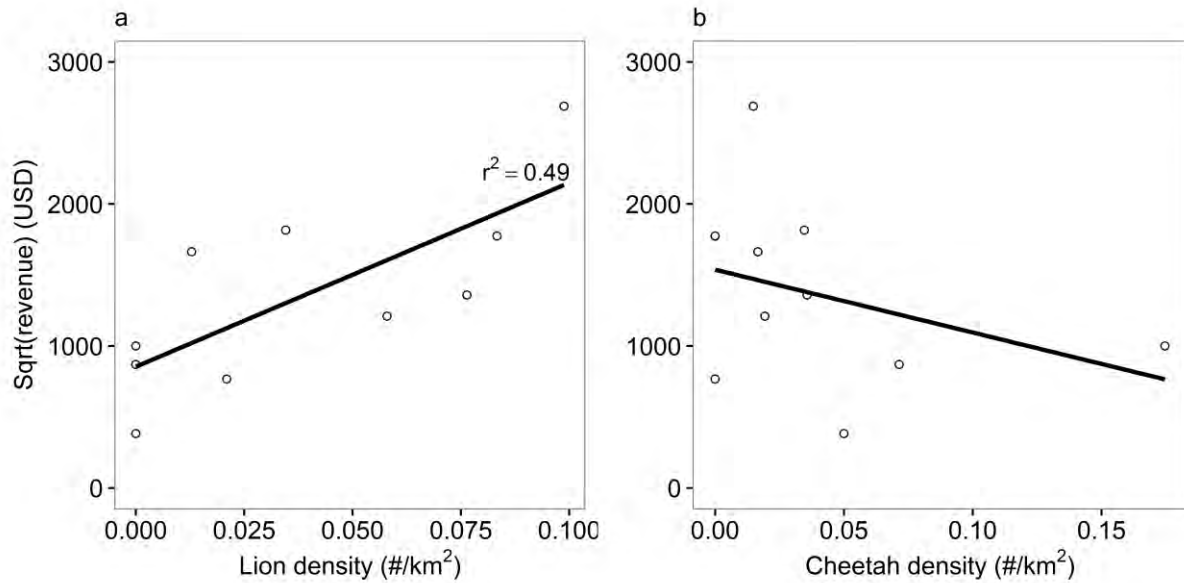




**Fig. 2.** Map of the Western and Eastern Cape Provinces of South Africa displaying the 22 surveyed Private Land Conservation Areas that stocked large predators, with 12 supporting free-roaming (“free”) large predators, and 10 supporting captive large predators.

The managers of all predator-present PLCAs rated profit generation to be an important (Likert rating  $> 3$ ) objective, with 75% rating it as very important (Likert rating = 5). Profit generation was rated as a significantly more important objective by the managers of predator-present PLCAs, compared with predator-absent PLCAs ( $mean_{present} = 4.8 \pm 0.1$ ,  $mean_{absent} = 3.7 \pm 0.2$ ;  $W = 397.5$ ,  $p = 0.02$ ). PLCA revenue generation was used to inform all management decisions on 33% of predator-present PLCAs, and was used to inform most management decisions on a further 50% of these PLCAs.

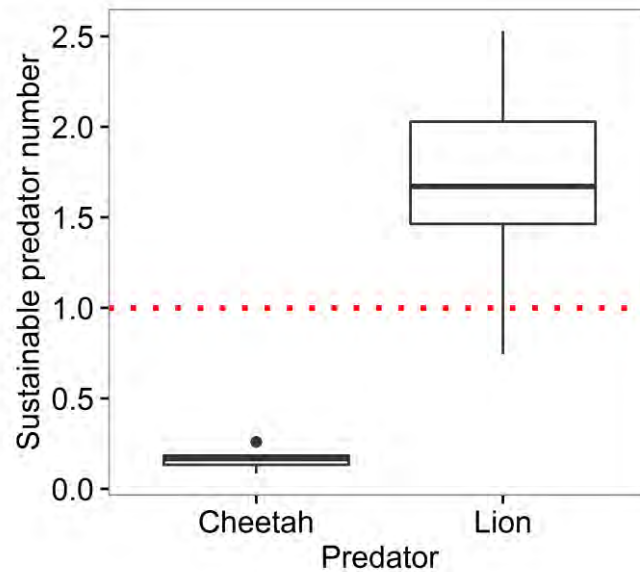
Predator-present PLCAs generated greater ecotourism revenues ( $mean = \$2,224,495 \pm 655,650$ ) than did predator-absent PLCAs ( $mean = \$170,500 \pm 85,678$ ;  $W = 355$ ,  $p < 0.001$ ). On predator-present PLCAs, lion density explained 49.3% of the variation in ecotourism revenue ( $F = 9.77$ ,  $n = 10$ ,  $p = 0.01$ ), with ecotourism revenue (square root transformed) increasing with increasing lion density ( $\beta = 12954 \pm 4145$ ,  $t = 3.39$ ,  $p = 0.01$ ; Fig. 3a). Cheetah density was not a significant predictor of ecotourism revenue ( $F = 1.09$ ,  $n = 10$ ,  $p = 0.33$ ; Fig. 3b).



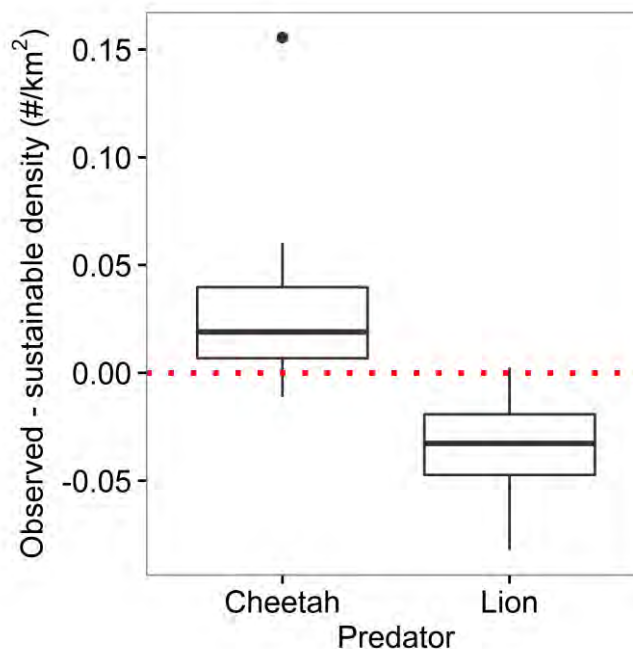
**Fig. 3.** The relationship between ecotourism revenue and (a) lion density, and (b) cheetah density on 10 Private Land Conservation Areas that stocked free-roaming large predators (five sites stocked both cheetah and lion, three sites supported cheetah only, and two sites supported lion only).

No PLCA that stocked free-roaming cheetah supported a sufficient biomass of preferred prey to sustain a single cheetah in the minimum area required by policy for the reintroduction of this species (i.e. 1,000 ha; Fig. 4). The majority of PLCAs that stocked free-roaming lion (7 out of 8) had sufficient preferred prey biomasses to sustain at least one lion in the minimum area required by policy (i.e. 2,000 ha), and were capable of supporting  $1.7 \pm 0.2$  lion per 2,000 ha on average (Fig. 4).

On PLCAs that stocked free-roaming cheetah, observed cheetah stocking rates were significantly above the sustainability threshold ( $W = 3$ ,  $n = 8$ ,  $p = 0.04$ ; Fig. 5), with just two out of eight of these PLCAs supporting a sustainable density of cheetah. On PLCAs that stocked free-roaming lion, observed lion stocking rates were significantly below the sustainability threshold ( $t = 3.52$ , d.f. = 7,  $p = 0.01$ ; Fig. 5), with all PLCAs supporting a sustainable density of lion. Predator contraception took place on 80% and 83% of sustainably and unsustainably stocked PLCAs, respectively. Predator sales/relocations took place on all predator-present PLCAs. Predator diet was not supplemented on any PLCAs supporting sustainable predator densities, while predator diet was supplemented on 67% of PLCAs supporting unsustainable predator densities. Similarly, game were introduced at least once every five years on just 20%, compared with 83%, of PLCAs supporting sustainable versus unsustainable predator densities, respectively.



**Fig. 4.** Summary statistics across Private Land Conservation Areas that stocked free-roaming cheetah and lion, of the number of predators that can be sustainably supported in the minimum area required by policy (cheetah: 1,000 ha; lion: 2,000 ha). Lines, boxes, error bars, and circles show medians, interquartile ranges, minima, and maxima (excluding outliers), and outliers (that deviate from the median by  $> 1 \times$  the interquartile range), respectively. Sustainable numbers were determined using available biomass ( $\text{kg}/\text{km}^2$ ) of preferred prey. The red dashed line indicates the threshold above which more than one individual can be sustained in the minimum required area.



**Fig. 5.** Summary statistics across Private Land Conservation Areas (PLCAs) that stocked free-roaming cheetah and lion, of the difference between the observed predator density on a PLCA and the density of predators that can be sustainably supported on that PLCA. Lines, boxes, error bars, and circles show medians, interquartile ranges, minima, and maxima (excluding outliers), and outliers (that deviate from the median by  $> 1 \times$  the interquartile range), respectively. The dashed red line indicates the threshold above which observed predator density is unsustainable.

## 5.4 Discussion

With greater ecotourism revenues generated on PLCAs where free-roaming large predators are present, there are clear financial incentives to stocking large predators. The managers of land supporting free-roaming large predators stated that revenue influenced most or all of their management decisions and rated profit generation to be a more important objective than the managers of land that did not support large predators. Financial incentives extend beyond the stocking of large predators to the population management of specific species. There are incentives to stock lion at high densities, with a positive relationship evident between lion density and revenue generated from ecotourism. In contrast, cheetah density had no effect on ecotourism revenue. These differences are supported by previous research on tourist preferences; lion rank as a more desirable species to see than cheetah (Di Minin et al. 2013; Maciejewski & Kerley 2014a). Lion are a member of the “Big Five”, a term coined by hunters as the five most difficult animals to hunt on foot, but latterly an important catch-phrase adopted by the safari industry to market Africa’s “most charismatic” species (Di Minin et al. 2013). I have not assessed the mechanism behind this observed relationship between lion density and revenue, and it is therefore important to note that (a) lion density may correspond with other important visitor pull factors, and (b) with a greater sample size I may be able to detect a threshold above-which increased lion density no longer improves visitor sighting success rates and thereby revenues, as seen with elephants (Maciejewski & Kerley 2014b).

A potential mismatch exists between financially-desirable and ecologically-sustainable lion densities, yet in actuality this mismatch did not appear to drive predator management, contrary to my prediction. Despite the financial incentives to stock lion at high densities, observed lion densities were sustainable in relation to available prey biomass. Due to their high reproductive potential, lion and cheetah numbers can increase rapidly when introduced onto small, fenced reserves with abundant and naïve prey, necessitating intensive management, such as relocation, contraception and/or culling (Hunter 1998; Tambling & du Toit 2005; Miller & Funston 2014). Frequent contraception and relocation actions were reported as predator management tools by PLCA managers. While these actions appeared effective in maintaining lion at sustainable densities, they were ineffective for cheetah population management. Cheetah occurred above densities that could be sustained on the biomass of preferred prey available on the majority of PLCAs.

Effective management of free-roaming large predators requires knowledge of what predator densities are sustainable. The minimum area policy guideline for lion, of 2,000 ha, is helpful in this regard. Sufficient prey biomasses were available to sustain at least one lion per

2,000 ha on the majority of PLCAs, supporting previous minimum area requirement estimates for lion (Creel & Creel 1997; Power 2003). With ecologically sound policy guidelines for lion area requirements corresponding with sustainable lion densities, it appears that policy can be a useful tool in promoting sustainable predator management. In contrast, not a single PLCA supported sufficient prey to sustain a single cheetah per 1,000 ha, thus questioning the soundness of this policy guideline (Department of Economic Development and Environmental Affairs 2008). Inappropriate regional guidelines corresponded with evidence of unsustainable cheetah management, as predicted. My findings suggest that a minimum area of 5,600 ha per cheetah (on average) is advisable, similar to that recommended in a country-wide study of cheetah area requirements in the presence of other large predators (Lindsey et al. 2011). Policy recommendations for cheetah minimum area requirements should therefore be revised in light of recent research findings (Lindsey et al. 2011).

While ecologically-sound minimum area guidelines can assist in the maintenance of sustainable large predator stocking densities, the effectiveness of these recommendations would likely be enhanced by a focus on prey requirements as opposed to area requirements, as well as consideration of the territorial habits and social structure of the species in question (see for example the South African National Norms and Standards for Elephant Management; Department of Environmental Affairs and Tourism (2008), which specify elephant social groups for reintroduction). The effectiveness of ecologically-sound management guidelines ultimately depends on the conservation authority's capacity to implement them. While the observed sustainability of lion densities suggests that the implementation of minimum area guidelines is currently effective, wildlife management policies receive substantial resistance from private landowners who perceive wildlife management restrictions to impair their ability to generate revenue (Cousins et al. 2010).

The overstocking of large predators can have substantial ramifications for ecosystem functioning. In fenced PLCAs, such as those in this study, ungulates are unable to escape predation and the consequence of predator population growth can be ungulate population declines and even collapses (Hunter 1998; Power 2003). PLCA managers can attempt to mitigate these impacts by frequently introducing additional prey, or by supplementing their predators' diets with meat acquired elsewhere (Lindsey et al. 2011; Miller et al. 2013). Both of these actions were more prevalent on PLCAs supporting unsustainable, as opposed to sustainable, predator populations. Elevated predator densities may, however, still have a significant negative impact on certain prey species, particularly smaller preferred prey species that are impractical to reintroduce and monitor, and secondary prey species that are usually

protected from predation through their scarcity relative to predator densities (Hayward 2011). For example, management actions in the Kruger National Park that increased habitat congruence between roan antelope *Hippotragus equinus* and lion caused the roan population to collapse as a result of increased predation (Harrington et al. 1999). In addition to directly influencing prey population dynamics, high predator densities can indirectly influence vegetation biomass and composition through the landscape of fear effect, altering prey habitat preferences and thereby the impact of herbivory in high risk habitats (Laundre et al. 2010; Tambling et al. 2012).

The predator-prey abundance models used to determine sustainable predator densities were developed in ecosystems that generally supported an intact large predator guild (Hayward et al. 2007c). In the absence of inter-guild competition for food, the application of these models to single-predator systems may result in an underestimation of sustainable predator densities. While I cannot exclude this potential bias, given that no alternative models exist, I show that management actions indicative of predator overstocking (feeding of predators and restocking of prey) are well aligned with my predictions of which predator populations are overstocked, suggesting my predictions are ecologically sound. It would be useful to further verify these predictions through evidence of declines in prey populations; such data were unfortunately unavailable for the study sites.

## **5.5 Conclusion**

Global ecosystem changes are associated with substantial declines in apex predator numbers (Estes et al. 2011), making effective large predator conservation efforts imperative. Debate about the conservation value of small, fenced, privately-owned and intensively managed areas for large predator conservation continues (Creel et al. 2013; Packer et al. 2013). For conservation authorities to develop effective solutions that facilitate sustainable predator management on private land, they must consider the strong and not necessarily beneficial multi-scale socioeconomic factors, such as international tourist preferences and regional policy recommendations, which influence private land management.

**Appendix 5A.** The density of free-roaming large predators on 12 Private Land Conservation Areas (PLCAs) in the Western and Eastern Cape Provinces of South Africa.

PLCA	Predator density (#/km <sup>2</sup> )		
	Cheetah	Lion	Spotted hyaena
1 (\$)	0.02	0.06	0
2 (\$)	0.01	0.10	0
3 (\$)	<b>0.02</b>	0.01	0
4 (\$)	<b>0.03</b>	0.03	0
5 (\$)	<b>0.04</b>	0.08	0
6 (\$)	<b>0.17</b>	0	0
7 (\$)	<b>0.05</b>	0	0
8 (\$)	<b>0.07</b>	0	0
9 (\$)	0	0.08	0.05
10 (\$)	0	0.02	0
11	0	0.01	0
12	present	0	0

NOTE: Bold values indicate densities that were found to be unsustainable (no sustainability estimate was available for spotted hyaena); “present” - predator was present but no count data were available; (\$) - sites for which ecotourism revenue was available.

### Abstract

There is increasing interest in the long-term effectiveness of conservation organizations. Their ability to adapt to change has been suggested as a key determinant of their effectiveness. Self-funded private land conservation areas (PLCAs), for example, may be vulnerable to a volatile tourism market. Over a third of financially-motivated PLCAs surveyed in South Africa were unprofitable, which raises questions about their ability to effectively adapt their budget ecotourism, hunting or “big game” ecotourism business models. Options for adaptation can be constrained by an organization’s initial conditions, a concept known as path dependence. I tested three hypothesized drivers of path dependence in PLCA business models: (1) size of land assets (game abundance is constrained by available land area); (2) extent of infrastructural assets (the introduction of “big” dangerous game requires substantial infrastructural investments); and (3) productivity (rainfall limits vegetation and thereby game abundance). I developed and ground-truthed a mechanistic PLCA model using simple rules for the abundance of game that can be sustained on a given land area and rainfall regime, infrastructure that can be developed with available capital, and resultant ecotourism/hunting revenue. Despite attempts by modelled managers to adapt to a more profitable business model, adopted business models after 13 years were differentiated by the initial size and extent of land and infrastructural assets, supporting hypotheses (1) and (2). Over a 50 year period, fewer managers that incorporated natural ecological variability into their management approach overcame path dependence due to higher inter-annual income variability, compared with those who maintained constant hunting rates and predator numbers. An organization’s initial conditions can cause it to become locked into a financially unviable business model, affecting its long-term sustainability. While resilience thinking calls for management that allows for natural ecological variability, the associated increase in income variability can perpetuate financially unviable business models.

### 6.1 Introduction

There is increasing interest in the likely long-term effectiveness of conservation organizations. While their ability to adapt to change has been suggested as a key determinant of their effectiveness (Kenward et al. 2011), factors influencing their adaptive capacity have only recently attracted attention (Baral 2013; Larson et al. 2014; Armsworth et al. 2015). A



system's adaptive capacity can be impeded if its developmental options are constrained by its initial conditions, a concept known as path dependence (Arthur 1994; Levin 1998; Carpenter & Brock 2008). In farming systems, for example, farmers can become trapped in financially unproductive agricultural practices, unable to accumulate the capital necessary to transition to a more viable alternative (Coomes et al. 2011). Potential mechanisms driving this organizational path dependence include the "asset hypothesis" and the "productivity hypothesis", where respective constraints in land holdings and equipment, and slow-growing woody vegetation, limit farmers to agricultural practices that perpetuate their financial vulnerability (Dercon 1998; Carter & Barrett 2006; Coomes et al. 2011; Naughton-Treves et al. 2011).

Path dependence may decay over time in some systems (Berkes 2007; Cumming et al. 2015), for example if a farmer gradually accumulates the capital necessary to purchase more land and thereby overcome the limitations to his agricultural options. Capital accumulation may be influenced by the adopted management strategy. "Command-and-control" refers to management that reduces natural ecological variability in a system in an attempt to increase its productivity and predictability (Holling & Meffe 1996). For example, farmers control fire regimes to maximize vegetation productivity (Anderies et al. 2002). In contrast, management that allows for natural variation (in fire frequencies and intensities, for example) may generate a more variable annual income. Systems with high income variability may be less likely to accumulate the capital necessary to overcome constraints on adaptation, given that the cost of servicing debt arising from negative income years (i.e. prime lending rate) is usually higher than the interest earned on an equivalent income in positive income years (i.e. short-term bond yield; see OECD 2016). The rate of path dependence decay experienced by an organization may therefore be influenced by the capital-accumulation potential of the adopted management strategy; I refer to this as the "management hypothesis".

Hypotheses regarding the emergence and decay of organizational path dependence can be used to assess potential drivers behind observed constraints on adaptation in the private land conservation sector. The management of private land for conservation is becoming increasingly recognized for its importance in global biodiversity conservation efforts (Fitzsimons & Wescott 2008; Gallo et al. 2009; Stolton et al. 2014). A third of financially-motivated private land conservation area (PLCA) managers surveyed in South Africa had adopted business models that were unprofitable (Chapter 3). It has been suggested that their ability to adapt to their economic environment is impeded by infrastructural and biophysical constraints that differentiate business models (Chapter 3; Hannan & Freeman 1984). While PLCAs supporting

predators and megaherbivores have the greatest income-generating potential, they require a game population large enough to sustain predators, which in turn depends on a sufficiently large and productive land area (Chapters 3 and 5). They further require a high investment in infrastructure in order to contain these dangerous animals, such as electrified fences around the property perimeter and accommodation areas (Department of Economic Development and Environmental Affairs 2008; Cape Nature Biodiversity Support Services 2014). Infrastructural and biophysical conditions, therefore, constrain a managers business model options. If the income-generating capacity of an adopted business model is low, then the PLCA may be unable to accumulate the capital necessary to overcome constraints and transition to a more profitable business model. Three alternative initial constraints may drive the documented “mismatch” between the proportion of PLCA managers that state profit to be an important objective and those that have adopted a profitable business model (Chapter 3). (1) The initial size of a PLCA limits the number of game and thereby predators that can be sustained (land assets hypothesis); (2) the initial investment in infrastructure limits the ability to introduce dangerous game (infrastructural assets hypothesis); and (3) the rainfall received by a PLCA limits the number of game and thereby predators that can be sustained (productivity hypothesis).

If path dependence arising from initial constraints determines a PLCA’s business model and thereby financial viability, the rate of decay in this path dependence will affect the ability of a self-funded PLCA to persist long-term. Wildlife is managed for optimal and stable financial returns on many PLCAs (Chapter 4). When managers focus on optimizing and stabilizing large mammal (game and sometimes predator) population numbers and the income derived from them (i.e. “command-and-control” management), slower-changing ecological variables such as vegetation composition can be overlooked, leading to large mammal overstocking and habitat degradation/ prey population declines (Chapters 4 and 5). In contrast, PLCAs that adopt an “ecological management” strategy, allowing large mammal numbers to fluctuate through natural climatic cycles, may generate a more variable annual income, while being more ecologically sustainable over longer time periods (Holling & Meffe 1996; Carpenter et al. 2015). I therefore apply the management hypothesis to predict that the rate of change in the proportion of PLCAs that transition to a more profitable business model over time will be greater on PLCAs undertaking command-and-control management than ecological management.

In order to test my hypotheses regarding path dependence and its rate of decay in private land conservation, I developed and ground-truthed a mechanistic PLCA model, which I ran from 2001 (the average startup year of PLCAs in the study sample) to 2013 under different

initial infrastructural and biophysical conditions and management strategies, allowing PLCA managers to adapt their business model every five years, dependent on accumulated capital and biophysical conditions. I assessed (a) whether differences existed between management strategies in inter-annual income variability and capital accumulation; (b) whether the final business models adopted by PLCAs were influenced by their initial size, infrastructural conditions and productivity (represented by rainfall), as evidence of path dependence; and (c), in order to compare the rate of decay in path dependence between management strategies, I extrapolated the model beyond the 2013 validation year and assessed the rate of change in the proportion of modelled managers adopting the most profitable business model between 2001 and 2050.

## **6.2 Methods**

### *6.2.1 Study region description and data collection*

I obtained data for the year 2013 from 52 commercial PLCAs in the Eastern and Western Cape Provinces of South Africa that rated profit generation as an important objective (Chapter 2). For each PLCA, data included (1) age and land area; (2) capital invested in land, infrastructure and game, and return on this investment; revenue generated from ecotourism, game sales and hunting; fixed and variable running costs, and proportion of income that is reinvested; (3) accommodation types, prices, number of beds and occupancy rates (explained in more detail in Chapter 3); (4) average annual rainfall; (5) game and predator stocking rates; and (6) whether ecological monitoring was undertaken (see methods described in Chapters 4 and 5).

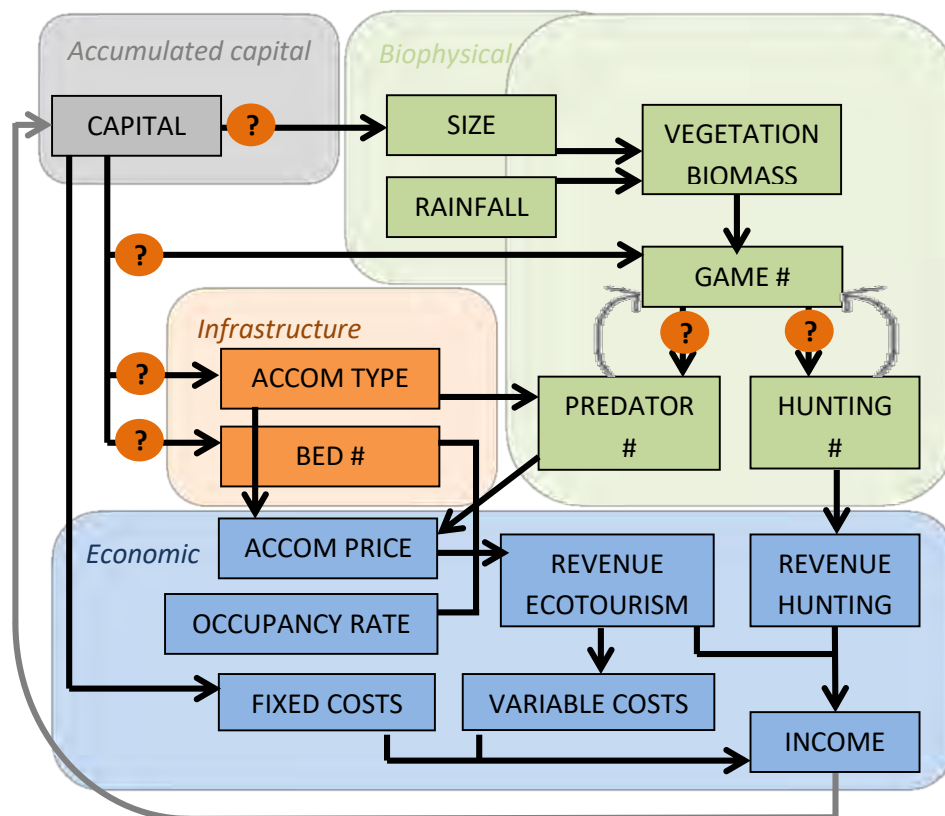
### *6.2.2 Model development*

*Parameters:* I developed and parameterized a mechanistic PLCA model (Fig. 1) using the following parameters: rainfall-vegetation-herbivore-predator relationships and parameters derived from the literature, national financial interest rates, regional game auction and hunting prices, and an understanding of capital and infrastructural constraints and pricing strategies obtained from PLCA managers. The details, values and sources of all parameters mentioned in the following model description are outlined in Table 1.

*Starting capital and land area:* I used 2001 as the model startup year because it was the average among study sites. Total capital investment at study sites in 2013 was normally distributed. Initial capital investment for simulated PLCAs in 2001 was selected randomly from this normal distribution, controlling for inflation and income reinvestment between 2001 and

2013. The modelled PLCA manager randomly chose what proportion of initial capital to spend on land, infrastructure and game. In the model managers purchased as much land as they could afford (Appendix 6A Q1; with the price of land (per square kilometre) following a power relationship with average annual rainfall).

*Infrastructure sub-system:* Accommodation types at study sites could be broadly assigned to three groups: lodges were expensive to build and to stay in; chalets were intermediately-priced; and campsites were cheap. As PLCAs with more expensive accommodation generated higher incomes (Chapter 3), given the capital available for infrastructure and the development cost per bed, the modelled PLCA manager built the most expensive accommodation and greatest number of beds that they could afford (Appendix 6A Q2-3).



**Fig. 1.** A hypothetical Private Land Conservation Area (PLCA), depicting relationships between available capital, the ecological system, infrastructure and capacity to generate an income. Black arrows indicate linkages between system elements, with arrow directions indicating causality. Grey arrows represent system feedbacks: hunting and predators influence game populations, income influences future PLCA development. Orange circles indicate management choices: what proportion of capital to spend on land, game and infrastructure, and how to manage game and predator populations. (# - number; accom – accommodation).

**Table 1.** Descriptions, values and sources of parameters used in the Private Land Conservation Area (PLCA) model.

Parameter	Value	Details (Source)
<i>Biophysical</i>		
$t$ (and $td$ )	2001	Year; average start-up year across study sites (Study site data).
$r$	Five annual rainfall patterns from 2001 to 2013	Rainfall [mm/year] (South African Weather Service data for the minimum, maximum, and 25%, 50% and 75% quartiles of observed average rainfall across study sites).
$gm$	102	Game size [kg]; average mass of stocked game (Skinner & Chimimba 2005).
$gr$	$1.5 * gm^{-0.36}$	Intrinsic growth rate of game population (Caughley & Krebs 1983).
$ge$	0.67	Proportion of game mass edible to a predator (Bissett & Bernard 2007).
$pq$	1442	Biomass requirements per predator [kg/year]; average between lion and cheetah (Owen-Smith & Mills 2008).
$pr$	0.56	Intrinsic growth rate of predator population (Fay & Greef 2006).
$v$	$0.02 * 0.02 * r^{1.69}$	Available herbivore metabolic biomass [kg/km <sup>2</sup> ] (Coe et al. 1976; Cumming & Cumming 2003).
$b$	$gm^{0.75}$	Metabolic biomass requirements per herbivore [kg/km <sup>2</sup> ] (Coe et al. 1976; Cumming & Cumming 2003).
<i>Economic</i>		
$i$	0.054	Average South African annual consumer price index (2001 to 2013; OECD 2016).
$pv$	$pv = (1 + i)^{(t-2013)}$	Controls financial variables for annual inflation (Ross et al. 2008).
$si$	0.08	Average South African short-term interest rate (2001 to 2013; OECD 2016).
$sl$	0.117	Average South African prime lending rate (2001 – 2013; South African Reserve Bank).
$sc$	Random number from normal distribution ( $\bar{sc} = 390$ ; $sd = 411$ ) * $pv$	Starting capital [R100,000]. Return on investment (ROI) controlled for by subtracting the average ROI at study sites in 2013 (3.5%) for each year that the modelled PLCA was operational (Study site data).
$pl$	$0.3 < pl < 0.8$	Proportion of starting capital spent on land (Randomly generated).
$pi$	$0.1 < pi < 1 - pl$	Proportion of starting capital spent on infrastructure (Randomly generated).
$pg$	$1 - pl - pi$	Proportion of starting capital spent on game (Randomly generated).
$cl$	$79,452 * pv * e^{0.0041 * \bar{r}}$	Cost of purchasing land [R/km <sup>2</sup> ] (Study site data).
$ca$	Lodge (l) = $5 * pv$ Chalet (ch) = $2.5 * pv$ Camping (c) = $0.5 * pv$	Cost of building accommodation [R100,000/bed]. Campsites assumed to accommodate 120 people (Estimated from discussion with several study site managers).
$cg$	$10,639 * pv$	Cost of purchasing game [R/animal]; average South African auction price of stocked game (North West University unpubl. data).
$ep$	lodge: $900 * pv$ ; chalet: $300 * pv$ , camping: $100 * pv$	Ecotourist accommodation price if predators are absent [R/bed/night]. (Camping price - average camping price at study sites; chalet and lodge prices - respective 25% and 75% quartile prices at study sites excl. camping).
$hp$	lodge: $3,393 * pv$ ; chalet: $2,785 * pv$	Hunter accommodation price [R/bed/night] (25% and 75% quartile study site values).
$ap$ & $\gamma p$	2,000 & 0.2, respectively	At sites supporting large predators there is a power relationship ( $y = ap * x^{\gamma p}$ ) between the number of predators $x$ and the price charged per visitor $y$ (Study site data).
$mfe, mfg,$ $mje, mjg,$ $cfe, cfq,$ $cje, cjg$	1.19, 0.85, 1.11, 1.10, 2.5, 0.33, 1.53, 1.44, respectively	Slope $m$ and y-intercept $c$ coefficients derived from relationships between invested capital and fixed running costs $f$ , and revenue and variable running costs $j$ under ecological $e$ and command-and-control $q$ management (Study site data).
$tr$	$21,305 * pv$	Price of hunting game [R/animal]; average hunting prices of stocked game (Hunting outfitter websites in the Western and Eastern Cape Provinces, South Africa).
$o$	0.3	Annual ecotourist accommodation occupancy rate in 2013 (Study site data).
$vi_t$	12 annual figures from 2001 to 2013	Visitor numbers to Addo Elephant National Park in the Eastern Cape Province of South Africa in year $t$ .

*Biophysical sub-system:* Five rainfall patterns were modelled. The herbivore metabolic biomass that a given land area in southern Africa can sustain (“carrying capacity”) can be determined from annual rainfall (Coe et al. 1976; Cumming & Cumming 2003). Modelled PLCA managers introduced the maximum number of large herbivores (“game”) that they could both afford and sustain (Appendix 6A Q4-6). I calculated the number of game that could be sustainably removed each year (“game offtake”) using the logistic equation (Caughley 1977; Starfield & Bleloch 1986). Initial predator carrying capacity was determined from game offtake. Modelled managers introduced predators at carrying capacity, provided that the correct infrastructure was in place (assuming only the most expensive accommodation provided the necessary infrastructure for introducing dangerous game, as observed at study sites; Appendix 6A Q7). The number of game that could be sustainably hunted/culled was modelled as the game offtake left after predators (if present) had consumed their annual requirement (Appendix 6A Q8). Hunters in the model did not camp, they required accommodation in either a lodge or a chalet, and below a game abundance of 90 commercial hunting was not viable and offtake was culled, as observed at study sites.

*Economic sub-system:* 2001 visitor prices were determined from 2013 prices at study sites, corrected for inflation. At sites supporting predators, there was a positive power relationship between the number of predators and the price charged per visitor (Appendix 6A Q9). At predator-absent PLCAs, hunters were charged a higher price than ecotourists (Appendix 6A Q9). Hunters and ecotourists did not reside on a PLCA concurrently (as seen at 67% of study sites). Visitor rates to Addo Elephant National Park in the Eastern Cape Province between 2001 and 2013 provided a proxy for annual variability in ecotourism occupancy rates (South African National Parks, unpubl. data; Maciejewski & Kerley 2014b). Ecotourism revenue was a function of the price charged per visitor per day, the number of beds available, and the occupancy rate (Appendix 6A Q10). Hunting revenue was a function of the number of game hunted, and the price per hunted animal (Appendix 6A Q10). Fixed running costs were positively related to total capital investment (e.g. money spent on salaries was proportional to lodge size and land area). Variable running costs were positively related to revenue (e.g. food and fuel costs varied with visitor numbers). These relationships were modelled separately for PLCAs that (a) undertook ecological management and (b) undertook command-and-control management (Appendix 6A Q10). Income (revenue minus running costs) could be positive or negative (Appendix 6A Q10).

*Annual model feedback and options for business model adaptation:* Each iteration of the model represented one year (Appendix 6A Q11). Accumulated capital at the start of each

year included capital available the previous year, minus capital spent in the previous year on PLCA development, plus income from the previous year (Appendix 6A Q12). Positive capital grew at the average annual short-term interest rate of 8.0%, while negative capital (i.e. debt) grew at the average annual prime lending rate of 11.7%. Modelled PLCA managers assessed development options every five years (guided by study site development timelines). If managers had accumulated capital, then they spent 70% on development (the average across study sites), and they chose randomly to (1) purchase as much additional land as they could afford, (2) upgrade and/or expand their accommodation, or (3) purchase as much game as they could afford and the PLCA could sustain (Table 2; Appendix 6A Q13). Game and predator numbers were modelled annually relative to rainfall, population growth and the adopted management strategy (Table 2; Appendix 6A Q14-16). Annual accommodation and hunting prices and development costs were corrected for inflation; occupancy rates varied relative to visitor rates to Addo Elephant National Park; ecotourism and hunting revenues, running costs and income were calculated for each model iteration (Appendix 6A Q17-18). Model simulations were run in Microsoft Excel (2010).

#### 6.2.3 *Model ground truthing*

I ran the model 200 times (100 random initial conditions under each management strategy) from 2001 to 2013, and recorded ten model-generated PLCA characteristics for the year 2013: invested capital (value of land, game and infrastructure), size, average annual rainfall, game and predator density, daily visitor price, bed number, revenue, running costs, and income. I converted South African Rands to United States Dollars using the average 2013/2014 South African Reserve Bank daily exchange rate (\$1 = R10.00). To assess the degree to which the ecological and development dynamics simulated by the model over the 13 year period resulted in emergent patterns that corresponded with those observed in reality, I compared the ten simulated PLCA characteristics in model year 2013 with the actual characteristics recorded for 52 study sites in 2013 (see section 6.2.1), using Mann-Whitney U tests due to non-normal data.

#### 6.2.4 *Assessing path dependence*

I categorized the 200 PLCA simulations in 2001 and 2013 into three “initial” and “final” business models, respectively: (1) big game PLCAs where predators were present; (2) hunting PLCAs where predators were absent and revenue was generated from hunting; and (3) budget PLCAs where no predators were present and no revenue was generated from hunting

(see Chapter 3). I assessed whether the final business models adopted by PLCAs in 2013 differed in their initial (year 2001) rainfall, land area and investment in infrastructure, using Kruskal-Wallis H tests followed by Mann-Whitney U tests, due to non-normal data. I further compared income and return on investment (ROI; income divided by total capital investment) in year 2013 between final business models.

**Table 2.** Large mammal management decisions made by modelled Private Land Conservation Area (PLCA) managers adopting ecological and command-and-control management strategies.

Management decision	Management strategy	
	Ecological	Command-and-control
Number of game that can be introduced in a development year	Rainfall and vegetation are monitored annually and, provided sufficient capital is available, the game population is augmented up to the current game carrying capacity (Appendix 6A Q13).	Rainfall and vegetation are not monitored and, provided sufficient capital is available, the game population is augmented up to the initially-determined game carrying capacity, adjusted relative to any subsequent increases in PLCA size (Appendix 6A Q13).
Number of predators that can be introduced in a development year, provided that suitable infrastructure is in place	If no predators are present, predators are introduced at the current predator carrying capacity (Appendix 6A Q15).	If no predators are present, predators are introduced at the initially-determined predator carrying capacity, adjusted relative to any subsequent increases in PLCA size (Appendix 6A Q15).
Annual predator population management	The predator population grows or declines annually relative to game abundance (Appendix 6A Q15).	Predators are maintained at a constant number through introductions, sales and/or contraception (Appendix 6A Q15).
Annual game offtake	If the game population, subsequent to growth and predator kills, is above current carrying capacity, then these excess game are removed in addition to the offtake left after predator kills. If the game population, subsequent to growth and predator kills, is below 50% of carrying capacity, then no game are removed to allow for population growth (Appendix 6A Q16).	The same proportion of the game population that was removed in the first year is removed in each subsequent year (Appendix 6A Q16).

I performed F-tests to compare inter-annual variability in average annual income between management strategies (i.e. average income in year  $t$  divided by average income in year  $t - 1$ ) and Mann-Whitney U tests to compare accumulated capital between management strategies, categorizing PLCAs using initial business models. Accumulated capital was determined as the difference in invested capital between 2013 and 2001. For each management strategy and initial business model, I plotted the average annual simulated values of rainfall, size, investment in infrastructure, game number, hunted game number and predator number.



Finally, in order to assess path dependence decay, I ran the PLCA simulations from 2001 until 2050. Rainfall and occupancy rates from 2014 to 2050 were extrapolated using trends and variability observed in actual data between 2001 and 2013 (Table 1). A linear regression was fitted to the relationship between year and proportion of PLCAs adopting a big game business model (R package: stats; function: lm), for each management strategy. Plots of fitted and observed values and residuals were examined for deviations from the assumptions of homogeneity and normality. Adjusted coefficients of determination were used to assess model fit. Regression slopes were compared using a t-test.

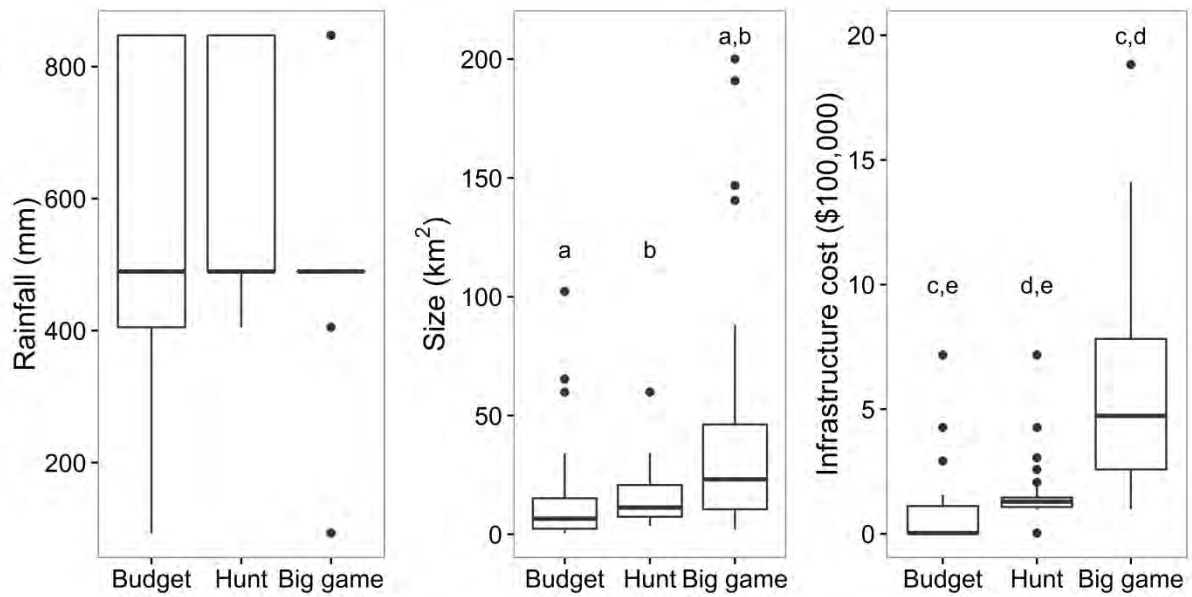
I compared ROI in 2050 between the three business models using a Kruskal-Wallis H test followed by Mann-Whitney U tests, due to non-normal data. Statistical analyses were performed in the statistical programme R (R Development Core Team 2016) at a significance level of  $\alpha = 0.05$ . Sequential Bonferroni corrections were used to correct for multiple comparisons (Rice 1989).

### 6.3 Results

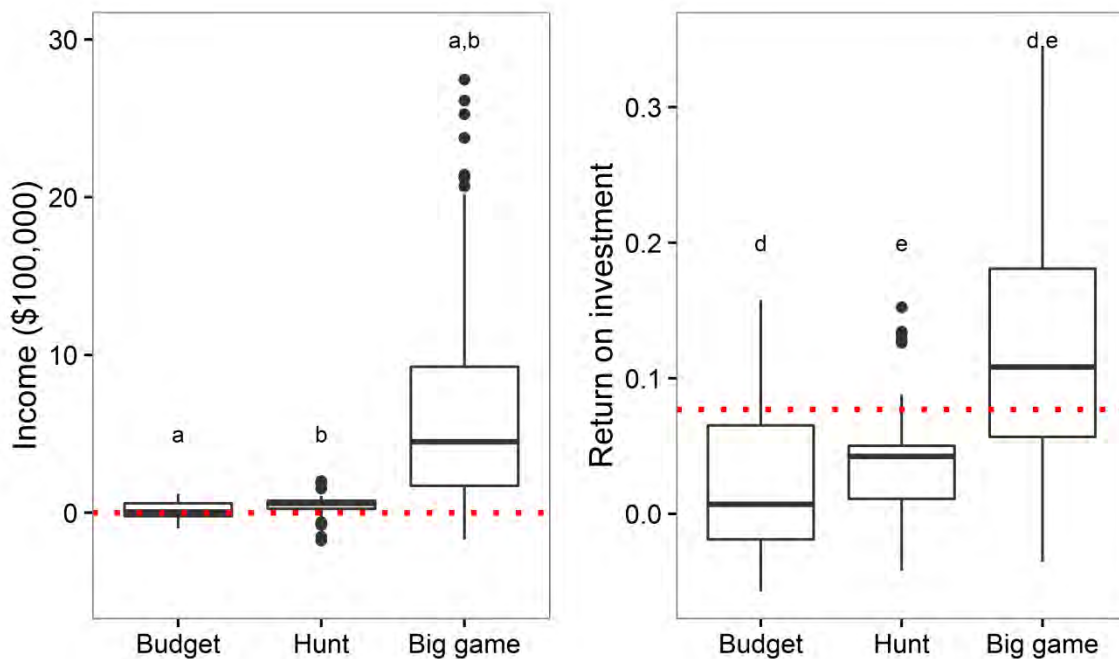
After a 13 year simulation period ending in 2013, the emergent values for invested capital, size, annual rainfall, game and predator density, daily visitor price, bed number, revenue, running costs, and income of 200 simulated PLCAs did not differ significantly from actual characteristics recorded for the 52 study sites in 2013 (Appendix 6B). This suggests that the model provides a reasonable approximation to real-world trends.

The three final business models adopted by simulated PLCAs in 2013 did not differ significantly in their initial annual rainfall ( $K = 0.6, p = 0.7$ ; Fig. 2). In contrast, the three final business models differed in their initial starting size and investment in infrastructure ( $K = 37.5, p < 0.001$  and  $K = 130.9, p < 0.001$ , respectively; Fig. 2). PLCAs that adopted a budget or hunting business model in 2013 were characterized by a lower initial size and investment in infrastructure than those that adopted a big game business model (Fig. 2). PLCAs which adopted a budget business model in 2013 were further characterized by a lower initial investment in infrastructure than those that adopted a hunting business model (Fig. 2).

Income and ROI in 2013 differed significantly between the final business models adopted by simulated PLCAs ( $K = 99.6, p < 0.001$  and  $K = 63.6, p < 0.001$ , respectively). Big game PLCAs were more profitable than both hunting PLCAs and budget PLCAs, and generated a larger ROI (Fig. 3).



**Fig. 2.** Comparison of Private Land Conservation Area (PLCA) initial conditions in 2001 between the final business models adopted by simulated PLCAs in 2013. Lines, boxes, error bars, and circles show medians, interquartile ranges, minima and maxima (excluding outliers), and outliers (that deviate from the median by  $> 1 \times$  the interquartile range), respectively. Corresponding letters indicate significant differences between business models (a.  $W = 1333$ ,  $p < 0.001$ ; b.  $W = 1250$ ,  $p < 0.001$ ; c.  $W = 175$ ,  $p < 0.001$ ; d.  $W = 258$ ,  $p < 0.001$ ; e.  $W = 490$ ,  $p < 0.001$ ).

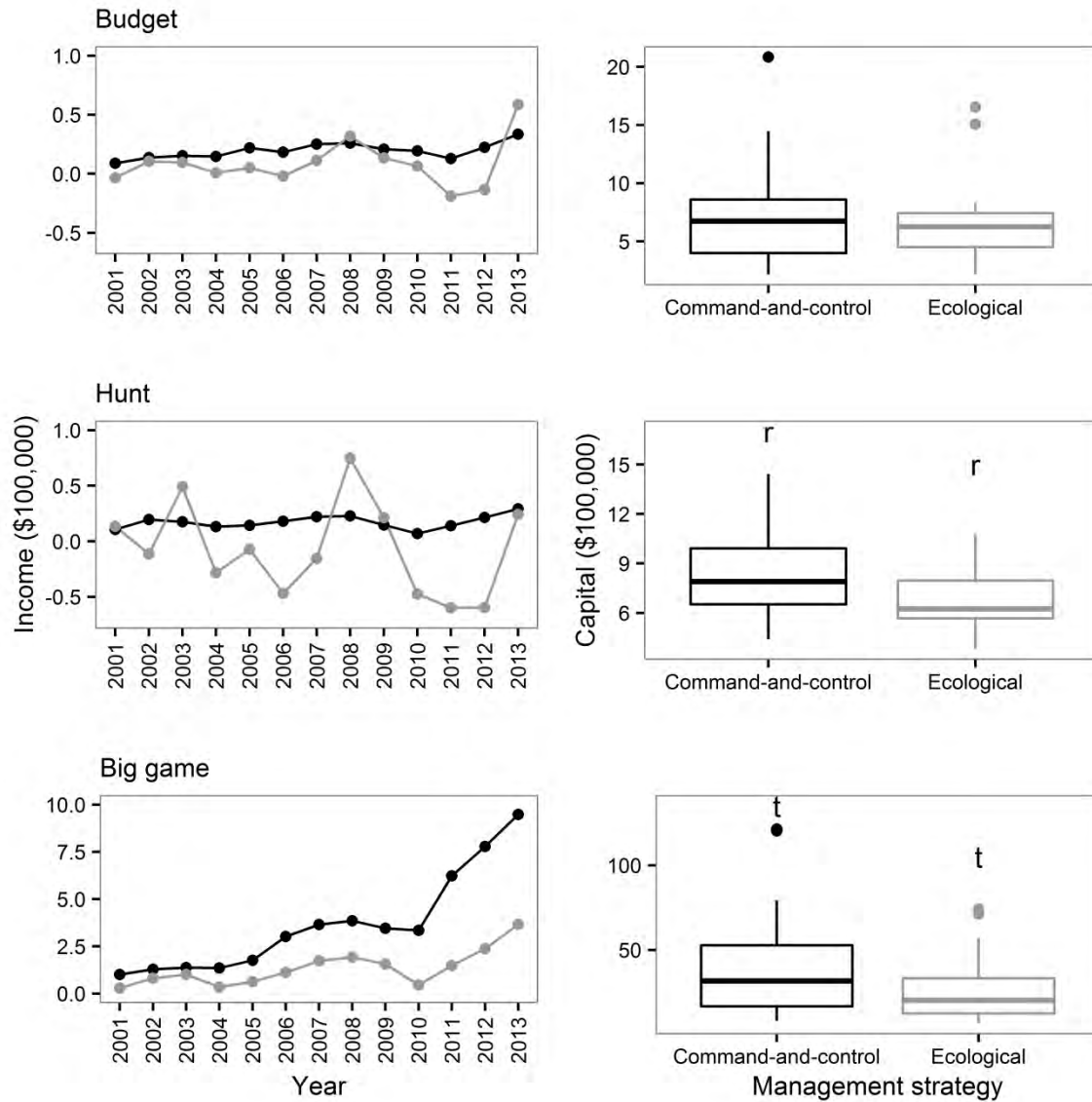


**Fig. 3.** Comparison of income and return on investment in 2013 between final business models adopted by simulated Private Land Conservation Areas. Lines, boxes, error bars, and circles show medians, interquartile ranges, minima and maxima (excluding outliers), and outliers (that deviate from the median by  $> 1 \times$  the interquartile range), respectively. Corresponding letters indicate significant differences between business models (a.  $W = 5330$ ,  $p < 0.001$ ; b.  $W = 3694$ ,  $p < 0.001$ ; d.  $W = 4877$ ,  $p < 0.001$ ; e.  $W = 3346$ ,  $p < 0.001$ ).

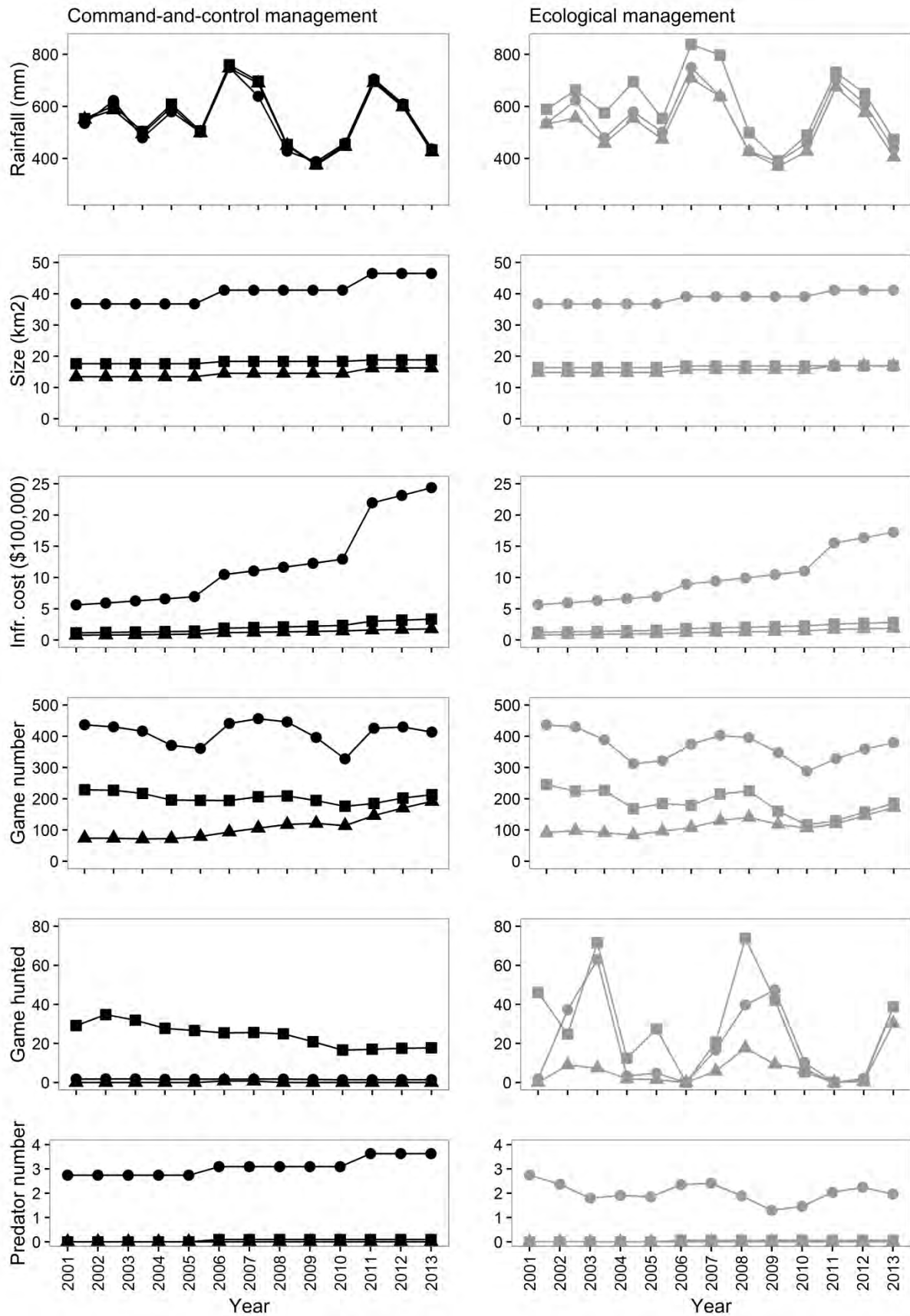
There was more inter-annual variability (“*V*”) in average income in PLCAs that employed an ecological (“*ecol*”), compared with a command-and-control (“*cnc*”) management strategy, for all three initial business models (Budget:  $V_{\text{ecol}} = 9.74$ ,  $V_{\text{cnc}} = 0.12$ ,  $F = 80.09$ ,  $p < 0.001$ ; Hunting:  $V_{\text{ecol}} = 8.29$ ,  $V_{\text{cnc}} = 0.22$ ,  $F = 37.81$ ,  $p < 0.001$ ; Big game:  $V_{\text{ecol}} = 0.77$ ,  $V_{\text{cnc}} = 0.08$ ,  $F = 9.09$ ,  $p < 0.001$ ; Fig. 4). Big game PLCAs that employed a command-and-control management strategy accumulated greater capital between 2001 and 2013 than did big game PLCAs that employed an ecological management strategy (Fig. 4). While the same trend was observed for hunting PLCAs, budget PLCAs accumulated similar capital regardless of management strategy (Fig. 4).

On average over a 13 year period, PLCAs that initially adopted the three different business models experienced similar annual rainfall patterns (Fig. 5). In contrast, PLCAs that had initially adopted a big game business model remained larger than those that initially adopted a hunting or budget business model, with higher investments in infrastructure and higher numbers of game and predators (Fig. 5). Predator numbers fluctuated to a greater extent on big game PLCAs that employed an ecological management strategy, compared to a command-and-control management strategy (Fig. 5). Similarly, the number of game hunted annually fluctuated to a greater extent on hunting PLCAs that had employed an ecological management strategy, compared to a command-and-control management strategy (Fig. 5).

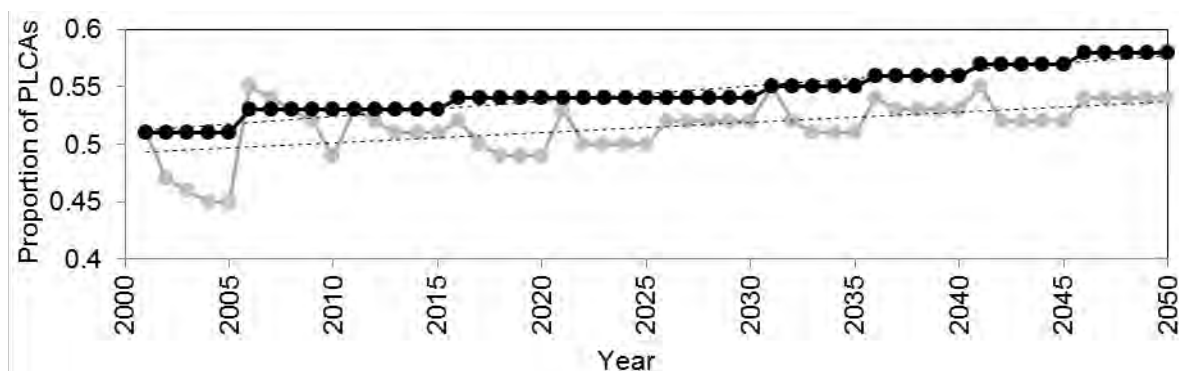
Having validated the model to a 13-year time horizon, I then extrapolated beyond my validation period to explore potential decay in path dependence. By the year 2050, big game PLCAs were still generating greater returns on investment than hunting and budget PLCAs ( $W = 5622$ ,  $p < 0.001$ ;  $W = 3485$ ,  $p < 0.001$ , respectively;  $\text{ROI}_{\text{Big game}} = 0.19 \pm 0.01$ ;  $\text{ROI}_{\text{Hunt}} = 0.00 \pm 0.01$ ;  $\text{ROI}_{\text{Budget}} = 0.02 \pm 0.01$ ). Between 2001 and 2050, the proportion of command-and-control managed PLCAs that had adopted a big game business model increased by 7% ( $r^2 = 0.92$ ;  $F = 602.01$ ,  $n = 50$ ,  $p < 0.001$ ). By contrast, the proportion of ecologically managed PLCAs that had adopted a big game business model increased by only 3% ( $r^2 = 0.30$ ;  $F = 22.18$ ,  $n = 50$ ,  $p < 0.001$ ). The rate of increase in the proportion of PLCAs adopting a big game business model was greater for command-and-control managed PLCAs than ecologically managed PLCAs ( $t = 1.99$ , d.f. = 96,  $p = 0.049$ ; Fig. 6).



**Fig. 4.** Average annual income between 2001 and 2013, and average capital accumulated by 2013 (total capital investment in 2013 minus initial capital investment in 2001), for 200 simulated Private Land Conservation Areas adopting three initial business models (budget, hunting and big game) and two management strategies (command-and-control management strategy represented in black, ecological management strategy represented in grey). Corresponding letters indicate significant differences between management strategies (r.  $W = 224$ ,  $p = 0.04$ ; t.  $W = 1851$ ,  $p < 0.01$ ).



**Fig. 5.** Average biophysical- and infrastructure-related values for simulated Private Land Conservation Areas over 13 years, according to management strategy and initial business model (● big game; ■ hunting; ▲ budget). (infra. cost – investment in infrastructure).



**Fig. 6.** Proportion of 100 simulated command-and-control managed Private Land Conservation Area (PLCAs; black dots and line) and 100 simulated ecologically managed PLCAs (grey dots and line) that adopted a big game business model between 2001 and 2050. Regression lines indicated by dashed black lines.

## 6.4 Discussion

Patterns in the observed characteristics of 52 PLCAs in 2013 were effectively simulated through simple rules for (1) how game and predator populations are managed and fluctuate relative to environmental conditions over time, (2) how income is generated relative to available game, predators and infrastructure, and (3) how PLCA managers expand their land and develop their infrastructure according to the accumulation of capital (Fig. 1). These simulations illustrate that initial organizational constraints can have a lasting influence on the ability of managers to adapt their PLCAs. PLCAs supporting large predators had the largest income-generating capacity (as observed in reality; Chapter 3). While simulated PLCA managers attempted to adapt to this business model, PLCAs that initially lacked the infrastructure necessary to introduce predators and the land area necessary to support large game populations and thereby predators, were largely unable to accumulate the capital required to develop their PLCAs to overcome these constraints. Path dependence in capital accumulation, arising from land and infrastructural asset constraints on business model options, is therefore a plausible mechanism behind the observed inability of PLCA managers to adapt their business models to their economic environment (Chapter 3). This finding supports theoretical discussions regarding the influence of infrastructure on the dynamics of social-ecological systems (Anderies & Janssen 2016). In contrast, I found no evidence for the productivity hypothesis. PLCA rainfall and thereby vegetation productivity did not constrain business model adaptation.

Less than 1.5% of PLCAs transitioned to the most profitable business model every five years. Assessing the likely sustainability of PLCAs with low income-generating capacity requires comparison between the time scales over which (a) path dependence decays and (b)

PLCA owners are able and willing to maintain a land use that is not meeting their objectives. Of the financially-motivated study site PLCAs that were not meeting their financial objectives in 2013, 82% stated that they would either attempt to adapt or sell their PLCA if they were not profitable within the next ten years (Chapter 3). With less than 3% of simulated PLCAs overcoming limitations on adaptation over this period, path dependence has the potential to be a strong driver of sustainability.

I only included data in this study from PLCAs that rated profit generation as an important objective, in order to make the assumption that managers attempt to adapt their PLCA to meet this objective. It is important to contextualize my findings, however, as not all PLCAs have financial objectives (Langholz 1996; Pasquini et al. 2010a; Selinske et al. 2015). While the majority of study site managers adopting big game and hunting business models rated profit generation as an important objective, more than half of the managers of budget PLCAs rated it as unimportant (Chapter 3). Path dependence in asset accumulation is unlikely to be an important driver of sustainability for PLCAs that lack financial objectives.

The ability of a PLCA to accumulate capital, and thereby overcome path dependence and adapt to a more profitable business model over a 50 year period, was influenced by the adopted management strategy. Big game and hunting PLCAs that allowed for natural ecological variability, by adjusting hunting rates based on vegetation monitoring and allowing predator populations to fluctuate naturally, accumulated less capital over time than those that maintained constant hunting rates and predator populations. The implementation of an ecological monitoring programme increases the running costs incurred by a PLCA (Chapter 4). In addition, allowing for natural ecological variability resulted in greater inter-annual income variability. This was particularly evident on PLCAs that generated revenue predominantly from consumptive wildlife uses (such as hunting). Allowing for natural fluctuations in game populations directly influences hunting rates, which have a linear impact on revenue. In contrast, non-consumptive wildlife uses, such as ecotourism, should be buffered to some extent from natural ecological variability because they offer an experience that is not linearly proportional to game numbers (Maciejewski & Kerley 2014b). The power relationship between prices charged to ecotourists and predator abundances (Table 1), however, means that substantial declines in predator populations do affect income on big game PLCAs (which supports the finding in Chapter 5 that ecotourism revenue is positively related to predator density). High income variability and the resultant reduction in the rate of path dependence decay may present a significant challenge for PLCAs, if their sustainability is dependent on their ability to remain (or become) financially viable.

It is dogmatic in the resilience literature that management which allows for natural ecosystem variability promotes resilient social-ecological systems (Holling & Meffe 1996; Biggs et al. 2012; Carpenter et al. 2015). I emphasize that an important outcome of allowing for natural variability in a managed natural resource is a corresponding increase in income variability. In the organizational literature, high income variability is considered an indicator of high risk in an organization (Gabriel & Baker 1980; Miller & Bromiley 1990). Therefore, the generally acknowledged trade-off between managing a natural resource for short-term productivity/stability and longer-term resilience may in fact be a more severe trade-off between financial and ecological vulnerability. Building resilience in such systems requires creative ways of managing the financial variability that arises from ecological variability, such as providing natural resource organizations with low interest rates on debt incurred in negative-income years.

The model developed in this study has several notable assumptions. Firstly, I assume that the prices paid by visitors and hunters vary through time with inflation rates. However, this may not always be the case. For example the exchange rate and/or competition between PLCAs may influence what visitors are willing to pay. International versus local markets and ecotourism versus hunting markets could be affected by these external drivers in different ways. The most profitable business model today may, therefore, not necessarily be the most profitable business model in the future. I emphasize that the message of this study is that path dependence in capital accumulation can constrain the adaptive capacity of an organization when asset constraints segregate business models, and not that big game PLCAs will continue to generate the greatest income indefinitely. Secondly, the incorporation of ecological or financial thresholds into the model was beyond the scope of this study. Command-and-control management can result in game overstocking (Chapter 4), which may ultimately influence vegetation productivity and composition (Seymour et al. 2010), and thereby affect both the ecological system and its income-generating potential. Similarly, I did not include financial thresholds, such as the number of years that an owner will sustain an unprofitable PLCA before they sell or change land-use. Our understanding of the effects of path dependence on PLCA sustainability would benefit from the incorporation of such thresholds.

## **6.5 Conclusion**

Initial differences in the assets of a conservation organization can determine what business model is adopted, and thereby the income that is generated and the capital that is accumulated. When financial viability is an important consideration, constraints imposed by



initial assets may set conservation organizations on paths towards collapse, by causing managers to become locked into financially unviable business models. While resilience thinking calls for management that allows for natural ecological variability, the associated increase in income variability can perpetuate this business model lock-in.

**Appendix 6A.** Questions asked and actions taken by modelled PLCA owners/managers in developing and then managing their PLCAs (refer to italicized parameter values and descriptions in Table 1).

*Start-up year:*

Question	Answer	Rationale
1. What size PLCA do I buy?	$size = size_{init} = (sc * pl) / cl$	An owner will buy the largest land area that he can afford.
2. What type of accommodation can I build?	$type_{accom} =$ If $sc * pi > ca_l * 6$ , then “lodge”, otherwise if $sc * pi > ca_{ch} * 6$ , then “chalet”, otherwise if $sc * pi > ca_c$ , then “camping”, otherwise “none”	Owners will build the most expensive accommodation type ( $type_{accom}$ ) that they can afford to build with at least 6 beds (i.e. 3 rooms; no study site accommodated <6 people).
3. How many beds can I build?	$bed.no =$ if $type_{accom} =$ “camping”, then 120, otherwise $(sc * pi) / ca$	Owners will build as many beds ( $bed.no$ ) as they can afford.
4. How many game can I sustain?	$game_{Kinit} = game_K = (v / b) * size$	Game carrying capacity ( $game_K$ ) is determined from available herbivore metabolic biomass, divided by metabolic biomass requirements per game individual (Coe et al. 1976; Cumming & Cumming 2003). This initial game carrying capacity estimate is determined by all modelled owners ( $game_{Kinit}$ ).
5. How many game can I afford?	$game_s = (sc * pg) / cg$	An owner can’t buy more game than he can afford ( $game_s$ ).
6. How many game do I introduce?	$count_{game} = \text{minimum}(game_s ; game_K)$	The number of game that are introduced ( $count_{game}$ ) is the maximum number that can be both sustained and afforded.
7. How many predators can I introduce?	$game.growth = gr * count_{game} * [1 - count_{game} / (game_K * 1.5)]$ $offtake_{gametotal} =$ if $count_{game} < 0.5 * game_K * 1.5$ , then $game.growth$ , otherwise $(gr * game_K * 1.5) / 4$ $predator_{Kinit} = predator_K = (offtake_{gametotal} * gm * ge) / pq$ $count_{predator} =$ if $type_{accom} =$ “chalet” or “camping”, then 0, otherwise $predator_K$	I assumed that game populations grow ( $game.growth$ ) according to the logistic equation (Caughley 1977). If a game population is greater than $0.5game_K$ , then the maximum number of individuals that can be sustainably removed each year ( $offtake_{gametotal}$ ; either by predators, hunting or culling) can be determined as the maximum sustainable yield (Caughley 1977; Starfield & Bleloch 1986). If the population is below $0.5game_K$ , then sustainable game offtake is game population growth (Caughley 1977; Starfield & Bleloch 1986). Given that game were observed to be stocked at $game_K * 1.5$ on average across study sites, through water and additional food provision (Chapter 4), I assumed game populations to grow relative to $game_K * 1.5$ instead of $game_K$ . To determine the number of predators that can be sustained on the available game offtake ( $predator_K$ ), I multiplied game offtake by the biomass per game individual edible to predators, and divided by the annual biomass requirements of the predator. This initial predator carrying capacity estimate is determined by all modelled owners ( $predator_{Kinit}$ ). Only PLCAs with a lodge can introduce predators. Study sites were found to overstock cheetah but understock lion relative to carrying capacity (Chapter 5). Therefore, provided that the correct infrastructure is in place, PLCAs introduced predators at $predator_K (count_{predator})$ .

8. How many game can I sustainably remove?	$\text{pred.kill} = (\text{count}_{\text{predator}} * pq) / (gm * ge)$ <p>(a) <math>\text{offtake}_{\text{gameleft}} = \text{if } \text{count}_{\text{game}} + \text{game.growth} - \text{pred.kill} &lt; 0.5 * \text{game}_K * 1.5, \text{ then } 0, \text{ otherwise } \text{offtake}_{\text{gametotal}} - \text{pred.kill}</math></p> <p>(b) <math>\text{offtake}_{\text{gameleft}} = \text{offtake}_{\text{gametotal}} - \text{pred.kill}</math></p> <p><math>\text{offtake}_{\text{hunt}} = \text{if } \text{count}_{\text{game}} &lt; 90, \text{ then } 0, \text{ otherwise if } \text{type}_{\text{accom}} = \text{"camping"} \text{ or "none"}, \text{ then } 0, \text{ otherwise } \text{offtake}_{\text{gameleft}}</math></p>	<p>The number of game that can be hunted/culled (<math>\text{offtake}_{\text{gameleft}}</math>) is the game offtake left after predators have consumed their annual requirement (<math>\text{pred.kill}</math>).</p> <p>(a) Ecological management: If the game population, subsequent to growth and predator kills is below <math>0.5\text{game}_K * 1.5</math>, none are removed to allow for game growth. Otherwise, maximum sustainable number are removed.</p> <p>(b) Command-and-control management: Maximum sustainable number removed. The observed minimum threshold for the number of game (<math>\text{count}_{\text{game}}</math>) necessary to hunt game offtake (<math>\text{offtake}_{\text{hunt}}</math>) for a fee is 90. Hunters require accommodation in either a lodge or a chalet.</p>
9. What can I charge per bed?	<p><math>\text{price}_{\text{accom}} = \text{if } \text{count}_{\text{predator}} = 0 \text{ and } \text{offtake}_{\text{hunt}} = 0, \text{ then } ep,</math>  otherwise, if <math>\text{count}_{\text{predator}} &gt; 0</math>, then <math>ap * (\text{count}_{\text{predator}}^{\wedge} \gamma p) * pv,</math>  otherwise <math>[(hp * \text{offtake}_{\text{hunt}} * 2) + (ep * o * \text{bed.no} * (365 - \text{offtake}_{\text{hunt}}))] / [(\text{offtake}_{\text{hunt}} * 2 + o * \text{bed.no} * (365 - \text{offtake}_{\text{hunt}}))]</math></p>	<p>I assumed that one game animal could be shot per day on a PLCA (guided by information from managers), and that each hunter brought a partner. Each animal hunted therefore represented 2 bednights. Hunters and ecotourists cannot reside on a PLCA at the same time; hunting days are subtracted from possible ecotourist days. Price charged (<math>\text{price}_{\text{accom}}</math>) is the average between price charged on hunting days and price charged on ecotourist days, weighted according to the number of bednights represented by hunters and ecotourists.</p>
10. How much do I earn?	<p><math>\text{occupancyeco} = o * vi_t / vi_{2013}</math></p> <p><math>\text{occupancy} = \text{if } \text{count}_{\text{predator}} = 0 \text{ and } \text{offtake}_{\text{hunt}} &gt; 0, \text{ then } [\text{offtake}_{\text{hunt}} * 2 + (\text{occupancyeco} * \text{bed.no} * (365 - \text{offtake}_{\text{hunt}}))] / (\text{bed.no} * 365), \text{ otherwise } \text{occupancyeco}</math></p> <p><math>\text{revenue}_{\text{eco}} = \text{price}_{\text{accom}} * \text{bed.no} * \text{occupancy} * 365</math></p> <p><math>\text{revenue}_{\text{hunt}} = \text{offtake}_{\text{hunt}} * tr</math></p> <p><math>\text{revenue} = \text{revenue}_{\text{eco}} + \text{revenue}_{\text{hunt}}</math></p> <p><math>\text{cost}_{\text{capital}} = \text{size} * cl + \text{count}_{\text{game}} * cg + \text{bed.no} * ca</math></p> <p><math>\text{cost}_{\text{fixed}} = \text{(a) } 10^{\wedge} [mfe * \log(\text{cost}_{\text{capital}}) - cfe]</math>  (b) <math>10^{\wedge} [mfq * \log(\text{cost}_{\text{capital}}) - cfq]</math></p> <p><math>\text{cost}_{\text{variable}} = \text{(a) } 10^{\wedge} [mje * \log(\text{revenue}) - cje]</math>  (b) <math>10^{\wedge} [mj q * \log(\text{revenue}) - cj q]</math></p> <p><math>\text{running.cost} = \text{cost}_{\text{fixed}} + \text{cost}_{\text{variable}}</math></p> <p><math>\text{income} = \text{revenue} - \text{running.cost}</math></p>	<p>Ecotourism occupancy rates estimated by standardizing average 2013 occupancy rates to study sites by visitor rates to Addo Elephant National Park. Occupancy rates are corrected according to the number of hunting bednights, see Q9. Revenues from ecotourism (eco) and hunting (hunt) are determined. Fixed running costs (<math>\text{cost}_{\text{fixed}}</math>) are related to the total value of the PLCA (<math>\text{cost}_{\text{capital}}</math>); variable costs (<math>\text{cost}_{\text{variable}}</math>) are related to total revenue. Fixed and variable costs were determined separately for PLCAs that (a) undertook ecological management and (b) undertook command-and-control management.</p>

---

Repeat for all subsequent years:

11. What year is it?  $t = t + 1$
12. How much capital do I have?  
 $\text{capital}_{\text{accumulated}} = \text{if } td = t - 1, \text{ then income, otherwise if } \text{capital}_{\text{accumulated}} > 0, \text{ then } \text{capital}_{\text{accumulated}} * si + \text{income, otherwise } \text{capital}_{\text{accumulated}} * sl + \text{income}$
13. Do I develop?  
 If  $t - td < 5$ , then  $\text{size} = \text{size}$ ,  $\text{count}_{\text{gameintro}} = 0$ ,  $\text{accom}_{\text{type}} = \text{accom}_{\text{type}}$ ,  $\text{bed.no} = \text{bed.no}$ ; go to Q14.  
 Otherwise set  $td = t$ . If  $\text{capital}_{\text{accumulated}} < 0$ , then  $\text{size} = \text{size}$ ,  $\text{count}_{\text{gameintro}} = 0$ ,  $\text{accom}_{\text{type}} = \text{accom}_{\text{type}}$ ,  $\text{bed.no} = \text{bed.no}$ ; go to Q14.  
 Otherwise choice = random one of "land", "game", "infrastructure". If choice = "land", then  $\text{size}_{\text{additional}} = (\text{capital}_{\text{accumulated}} * 0.7) / cl$ ,  $\text{size} = \text{size} + \text{size}_{\text{additional}}$ ,  $\text{count}_{\text{gameintro}} = 0$ ,  $\text{accom}_{\text{type}} = \text{accom}_{\text{type}}$ ,  $\text{bed.no} = \text{bed.no}$ ; go to Q14.  
 Otherwise if choice = "game", then  $\text{game}_s = (\text{capital}_{\text{accumulated}} * 0.7) / cg$ ,  
 (a) if  $\text{count}_{\text{game}} < \text{game}_K$ , then  $\text{count}_{\text{gameintro}} = \text{minimum}(\text{game}_s; \text{game}_K - \text{count}_{\text{game}})$ ,  
 (b) if  $\text{count}_{\text{game}} < \text{game}_{K\text{init}} * (\text{size} / \text{size}_{\text{init}})$ , then  $\text{count}_{\text{gameintro}} = \text{minimum}(\text{game}_s; \text{game}_{K\text{init}} * \text{size} / \text{size}_{\text{init}} - \text{count}_{\text{game}})$   
 $\text{capital}_{\text{develop}} = \text{capital}_{\text{accumulated}} - \text{count}_{\text{gameintro}} * cg$   
 If  $\text{capital}_{\text{develop}} = 0$ , then  $\text{accom}_{\text{type}} = \text{accom}_{\text{type}}$ ,  $\text{bed.no} = \text{bed.no}$ ; go to Q14.  
 Otherwise, if  $\text{accom}_{\text{type}} = \text{"lodge"}$ , then  $\text{accom}_{\text{type}} = \text{"lodge"}$ ,  $\text{bed.no} = \text{bed.no} + [\text{capital}_{\text{develop}}] / ca_l$ , go to Q14.  
 Otherwise if  $\text{accom}_{\text{type}} = \text{"chalet"}$  and  $[\text{capital}_{\text{develop}}] > ca_l * 0.5 * \text{bed.no}$ , then  $\text{accom}_{\text{type}} = \text{"lodge"}$ ,  $\text{cost}_{\text{accomupgrade}} = ca_l * 0.5 * \text{bed.no}$ ,  $\text{bed.no} = \text{bed.no} + [\text{capital}_{\text{develop}} - \text{cost}_{\text{accomupgrade}}] / ca_l$ ; go to Q14.  
 Otherwise if  $\text{accom}_{\text{type}} = \text{"chalet"}$ , then  $\text{accom}_{\text{type}} = \text{"chalet"}$ ,  $\text{bed.no} = \text{bed.no} + [\text{capital}_{\text{develop}}] / ca_{ch}$ ; go to Q14.  
 Otherwise if  $[\text{capital}_{\text{develop}}] > ca_l * 6$ , then  $\text{accom}_{\text{type}} = \text{"lodge"}$ ,  $\text{bed.no} = [\text{capital}_{\text{develop}}] / ca_l$ ; go to Q14.  
 Otherwise if  $[\text{capital}_{\text{develop}}] > ca_{ch} * 6$ , then  $\text{accom}_{\text{type}} = \text{"chalet"}$ ,  $\text{bed.no} = [\text{capital}_{\text{develop}}] / ca_{ch}$ ; go to Q14.  
 Otherwise  $\text{accom}_{\text{type}} = \text{"camping"}$ ,  $\text{bed.no} = \text{bed.no}$
14. How many game do I have?  
 $\text{game}_K = (v / b) * \text{size}$ , where  $r = r$  in year =  $t - 1$  and  $\text{size} = \text{size}$  in year =  $t - 1$ .  
 $\text{game.growth} = gr * \text{count}_{\text{game}} * [1 - \text{count}_{\text{game}} / (\text{game}_K * 1.5)]$   
 $\text{pred.kill} = (\text{count}_{\text{predator}} * pq) / (gm * ge)$   
 $\text{count}_{\text{game}} = \text{count}_{\text{game}} + \text{game.growth} - \text{pred.kill} - \text{offtake}_{\text{gameleft}} + \text{count}_{\text{gameintro}}$

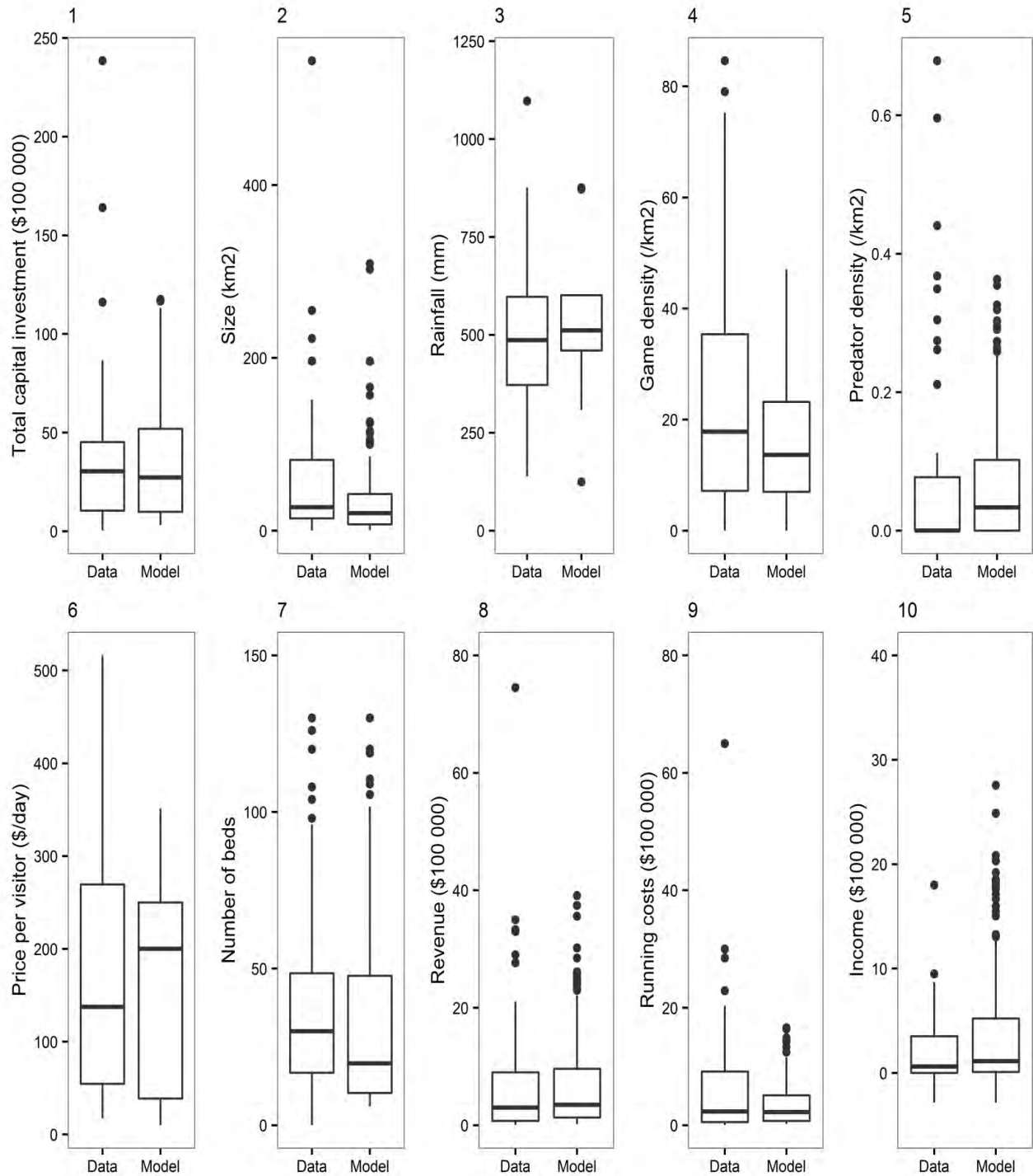
Accumulated capital ( $\text{capital}_{\text{accumulated}}$ ) is determined as capital from the previous year, minus capital spent in the previous year on PLCA development, plus income from the previous year.

Owners assess development options every five years. If owners have not accumulated any capital, then they do not consider developing for another five years. Otherwise owners spend 70% of accumulated capital on development, and they chose randomly to (1) purchase as much additional land as they can afford ( $\text{size}_{\text{additional}}$ ), (2) purchase as much game as they can afford up to the limit of (a) the current game carrying capacity or (b) the initial carrying capacity guideline adjusted relative to any subsequent increases in size ( $\text{count}_{\text{gameintro}}$ ), or (3) upgrade and/or expand their accommodation. If the manager decides to buy game but is not able to spend all 70% of capital on game purchase due to the upper threshold defined in (2), then this money ( $\text{capital}_{\text{develop}}$ ) can be spent on accommodation. I assume that the cost of upgrading from a chalet to a lodge ( $\text{cost}_{\text{accomupgrade}}$ ) is half the price of building a lodge from scratch. I assume that the cost of upgrading a campsite to a lodge or chalet is equal to the total costs of building a lodge or chalet, respectively. A PLCA upgrades from a chalet to a lodge if it has sufficient capital to upgrade all chalet beds. A PLCA upgrades from a campsite to a lodge or chalet if it has sufficient capital to build lodge or chalet accommodation for 6 people (see Q2).

Game number is determined at the start of each year, according to growth, kills and removals in the previous year. A game population grows according to the logistic equation, see Q7.

15. How many predators do I have?	$game_K = (v / b) * size$ , where $r = r$ in year = $t$ and $size = size$ in year = $t$ . $game.growth = gr * count_{game} * [1 - count_{game} / (game_K * 1.5)]$ $offtake_{gametotal} = \text{if } count_{game} < 0.5 * game_K * 1.5, \text{ then } game.growth, \text{ otherwise } (gr * game_K * 1.5) / 4$ $predator_K = (offtake_{gametotal} * gm * ge) / pq$ (a) $count_{predator} = \text{if } count_{predator} > 0, \text{ then } count_{predator} + count_{predator} * pr * (1 - count_{predator} / predator_K), \text{ otherwise if year} = td \text{ and } accom_{type} = \text{"lodge"}, \text{ then } count_{predator} = predator_K, \text{ otherwise } 0.$ (b) $count_{predator} = \text{if } count_{predator} > 0, \text{ then } count_{predator}, \text{ otherwise if year} = td \text{ and } accom_{type} = \text{"lodge"}, \text{ then } count_{predator} = predator_{Kinit} * (size / size_{init}), \text{ otherwise } 0.$	Predator number is determined at the end of each of year. See Q7. (a) If the PLCA is undertaking ecological management, the predator population grows/declines annually according to the logistic equation. If there are currently no predators and it is a development year, a manager can introduce predators at their current carrying capacity. (b) If the PLCA is undertaking command-and-control management, the predator population kept constant by sales and/or contraception and feeding. If there are currently no predators and it is a development year, a manager can introduce the initial carrying capacity of predators, adjusted relative to any subsequent increases in size.
16. How many game can I sustainably remove?	$pred.kill = (count_{predator} * pq) / (gm * ge)$ (a) $offtake_{gameleft} = \text{if } count_{game} + game.growth - pred.kill > game_K, \text{ then } (count_{game} + game.growth - pred.kill - game_K) + (offtake_{gametotal} - pred.kill), \text{ otherwise if } count_{game} + game.growth - pred.kill < 0.5 * game_K * 1.5, \text{ then } 0, \text{ otherwise } offtake_{gametotal} - pred.kill$ (b) $offtake_{gameleft} = offtake_{gametotal} - pred.kill$ $offtake_{hunt} = \text{if } count_{game} < 90, \text{ then } 0, \text{ otherwise if } type_{accom} = \text{"camping"} \text{ or } \text{"none"}, \text{ then } 0, \text{ otherwise } offtake_{gameleft}$	See Q8. (a) Under ecological management, game carrying capacity is determined each year. If the game population, subsequent to growth and predator kills is above its carrying capacity, then this excess number of game is removed in addition to the offtake left after predator kills. If the game population, subsequent to growth and predator kills is below $0.5game_K * 1.5$ , none are removed to allow for game growth. (b) Under command-and-control management, game carrying capacity is not determined each year, and the same proportion of the total game population is removed each year.
17. What can I charge / bed?	See Q9	
18. How much do I earn?	See Q10	

**Appendix 6B.** Comparison between data attributes recorded for 52 Private Land Conservation Areas in 2013, and attributes generated from a mechanistic model run from 2001 to 2013. No attributes are significantly different at a bonferroni-corrected  $\alpha = 0.005$  (1.  $W = 4412$ ,  $p = 0.98$ ; 2.  $W = 6468$ ,  $p = 0.007$ ; 3.  $W = 4780$ ,  $p = 0.4$ ; 4.  $W = 5973$ ,  $p = 0.03$ ; 5.  $W = 4220$ ,  $p = 0.1$ ; 6.  $W = 5455$ ,  $p = 0.4$ ; 7.  $W = 6315$ ,  $p = 0.02$ ; 8.  $W = 3727$ ,  $p = 0.7$ ; 9.  $W = 3756$ ,  $p = 0.5$ ; 10.  $W = 3251$ ,  $p = 0.2$ ).



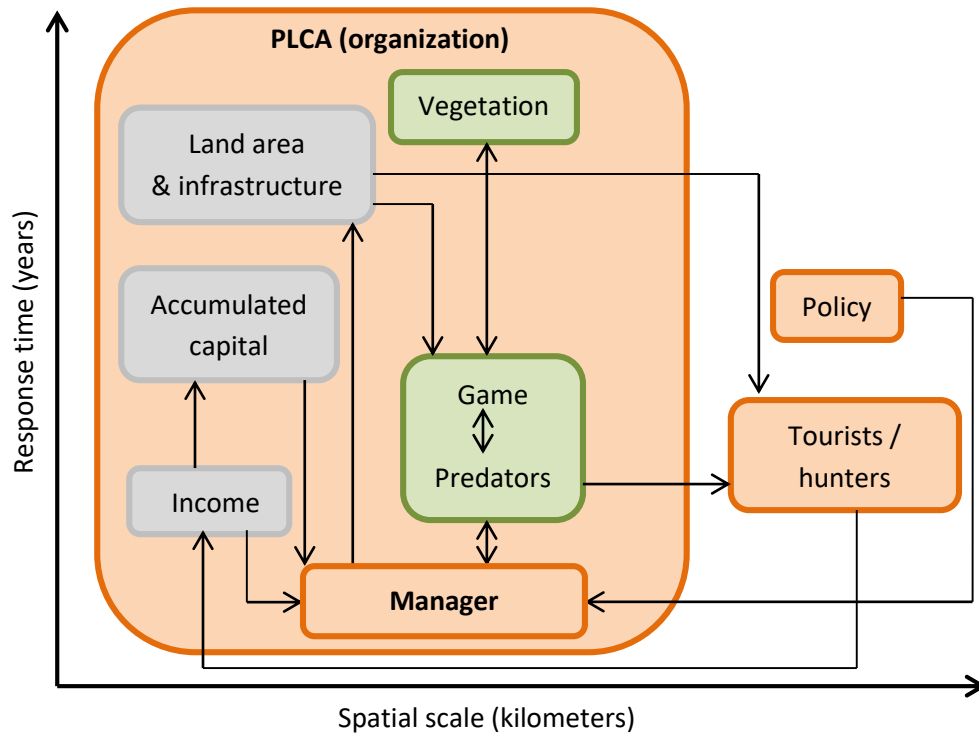
## CHAPTER 7: SYNTHESIS

---

The concept of a social-ecological system acknowledges the linked nature of people and ecosystems, and the importance of these linkages for humanity's well-being and sustainable development. Social-ecological systems research is a young and rapidly growing field of study, and several concepts remain poorly developed. Notably, in understanding the behaviour of social-ecological systems, much focus has been placed on the role of institutions that govern how natural resources should be managed, and the biophysical processes affected by this management. Somewhat less attention has been given to the role played by management organizations and natural resource managers themselves. In this thesis I have contributed to social-ecological systems theory through an in-depth investigation of the social-ecological interactions driving the management and sustainability of commercial Private Land Conservation Areas (PLCAs) in the Cape region of South Africa.

The objectives of this thesis were to assess *if*, *how* and *why* commercial PLCA managers (a) meet their financial objectives and (b) adopt unsustainable ecological management practices. I illustrate that PLCA profitability and management are influenced by interactions between natural resources and their resource systems, natural resource managers and their organizations, regional policies, and national and international tourists (Fig. 1). These interactions occur over multiple temporal, institutional and spatial scales (Fig. 1), and have important implications for the likely long-term sustainability of PLCAs, as I will synthesize in this chapter.

I first outline how I achieved my objectives, and the two primary contributions that this thesis makes to social-ecological systems theory. These contributions, as identified in Chapter 1, are (1) how ideas from organizational studies can be applied to understand patterns in the organizational strategies adopted by natural resource managers, and (2) how manager action-outcome feedbacks function as pivotal interactions in social-ecological systems (Fig. 1). I follow with a theoretical and practical perspective on governance in private land conservation, practical implications and suggestions arising from this study, and a reflection on the research approach. I conclude with a discussion on future research directions.



**Fig. 1.** Conceptual representation of the multi-scale, social-ecological components and interactions that characterize commercial Private Land Conservation Areas (PLCAs), as revealed by this thesis (Chapters 3 to 6). Ecological and social system components are represented in green and orange, respectively. Arrow directions indicate causality of interactions. The two focal system components studied in this thesis (the manager and their organization) are indicated in bold. Spatial scale represents the scale at which system components function (from game and predators occurring within a PLCA of several hundred square kilometers, to regionally-relevant policies, and tourists that live within the same country as a PLCA or up to several thousand kilometers away). Response time represents the time taken for system components to respond to internal or external changes (from predator and game abundances that change annually, to vegetation quality which can take decades to change; and from a PLCA manager which can respond to emergent issues within several months, to regional governments which may take several years or decades to respond with policy amendments). As this is a conceptual representation, box sizes and locations are intended to illustrate relative scales at which system units may operate, as opposed to providing precise estimates.

## 7.1 The application of organizational theories to a social-ecological system

PLCAs emerge from the motivations/objectives of individual landowners, often in the absence of external incentives, programmes or legislation (Stolton et al. 2014). Even when formal legal protection exists, it does not always ensure sustainability (see, for example, the occurrence of covenant breaches in Australia; Hardy et al. 2016). The sustainability of a PLCA is therefore likely to be influenced by its continued ability to meet its owner's objectives. Concerns have been

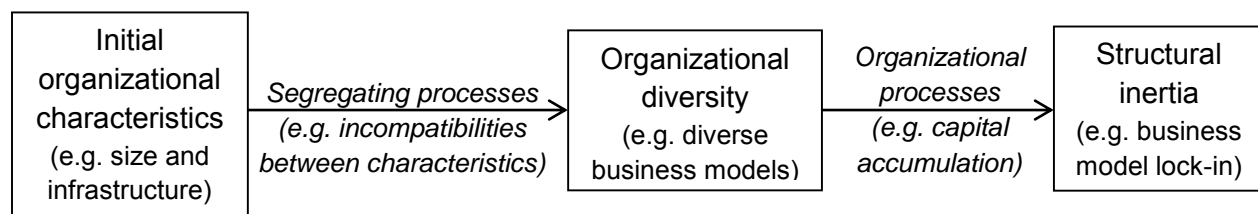


raised that the sustainability of commercial PLCAs may be contingent on their ability to become and/or remain financially viable (Langholz 1996; Langholz & Lassoie 2001; Pasquini et al. 2010b; Miller et al. 2013; Pegas & Castley 2014). The first objective of this thesis was therefore to investigate *if, how and why* the managers of commercial PLCAs meet their financial objectives. Almost a quarter of interviewed PLCA managers stated profit generation to be an important objective but were not currently achieving this objective (Chapter 3), and a diverse range of biophysical and socioeconomic PLCA characteristics influenced revenue-generation and profitability (Chapters 3, 4 and 5). In order to understand why this common “mismatch” existed between managers’ financial objectives and their PLCAs’ financial outcomes, I applied theories from organizational ecology.

PLCAs can be viewed as organizations, characterized not only by the resource units and systems within their boundaries, but by their ecological and business management objectives and strategies, infrastructure, and financial systems (Fig. 1; Chapters 3 and 6). Organizational ecology hypothesizes that organizations become segregated into distinct clusters sharing a common identity when there are incompatibilities between organizational characteristics that segregate the combinations of characteristics that can emerge and persist (Hannan & Freeman 1986; Ruef 2000). In support of this theory, distinct clusters of PLCAs were evident, which displayed unique combinations of socioeconomic and ecological characteristics, and differed in their income-generating potential (Chapter 3). These “business models” were segregated by meaningful incompatibilities between certain characteristic combinations, such as small size and large number of game species, or hunting activities and the presence of large predators.

Organizational ecology further proposes that elements of organizational identities (such as business models) can be subject to structural inertia, with limited ability to adapt at an appropriate rate to changes in their environment (Hannan et al. 2004; Stieglitz et al. 2016). The theory of path dependence is a proposed mechanism that can lead to structural inertia in organizations (Sydow et al. 2009; Heine & Rindfleisch 2013). Path dependence, in the organizational context, is defined as historical events, which may, under certain conditions lead to self-reinforcing processes and result in organizational lock-in (Sydow et al. 2009). Applying these theories to PLCAs through the development of a mechanistic model, I found evidence that initial investments in land area and infrastructure determine which business model can be adopted by a manager, and limitations in the capital that can be accumulated from certain business models prevent managers from

overcoming the socioeconomic and ecological incompatibilities that separate business models, leading to inert business models that do not meet their managers' financial objectives (Figs. 1 and 2; Chapter 6). These organizational limitations on the ability of PLCA managers to adapt to their economic environment have important implications for PLCA sustainability. Managers of over 80% of mismatched PLCAs stated that they would not continue to finance an unprofitable organization indefinitely, and would either sell or attempt to adapt if they do not manage to achieve their financial objectives in the next ten years (Chapter 3). Less than 3% of simulated PLCAs overcame limitations on adaptation over this period (Chapter 6). "Rational routes to collapse" (Peterson et al. 2003) may therefore arise in social-ecological systems when initial, rational choices of how to manage and conserve a natural resource in a given socioeconomic environment lead to inert organizational structures that are unable to adapt effectively to changing socioeconomic conditions.



**Fig. 2.** Organizational theories regarding the mechanisms that drive patterns of organizational diversity and lock-in.

The ability to adapt to change has been suggested as a key determinant of the effectiveness of conservation organizations (Clarke & McCool 1996; Kenward et al. 2011). Empirical assessments of the adaptive capacity of conservation organizations are scarce, as are hypotheses regarding the determinants of this adaptive capacity (but see Baral 2013; Larson et al. 2014; Armsworth et al. 2015). In contrast, this topic has received considerable attention in the organizational sciences (see review by Heine & Rindfleisch 2013). This thesis provides a unique illustration of how organizational sciences can contribute to developing hypotheses for the behaviour of organizations in governing social-ecological systems. For example, nonprofit organizations within the biodiversity conservation sector in the United States were found to have little capacity to adapt their financial management to economic change (Larson et al. 2014). It was suggested that this may be because (a) changes to funding processes and conservation activities occur at time scales too long to be detected by the study; or (b) biodiversity conservation nonprofits

do not prioritize responsiveness to changing economic conditions as an organizational objective (Larson et al. 2014). Ideas from organizational ecology enable me to propose a third hypothesis, that conservation nonprofits experience structural inertia in their spending practices (for example, through path dependency in land purchase, rigid management strategies, etc.), which impede their ability to adapt (Fig. 2).

Patterns and processes unique to social-ecological systems may provide novel perspective on organizational theories. Socioeconomic processes (such as demand and revenue) can change over short time periods, while ecological processes like habitat alteration or trophic cascades generally change over much longer time scales (Walker et al. 2006; Cumming et al. 2015). Therefore, when income generation is an important driver of management in a social-ecological system (such as a farm, fishery or commercial PLCA), managers may more readily attempt to adapt their management to socioeconomic processes than to ecological processes (Chapter 4; Cumming et al. 2015). If these adaptations are detrimental to slower-changing ecological processes (see Chapter 4, for example), then the social-ecological system becomes gradually less resilient to the larger shocks that may eventually emerge from ecological feedbacks (Cumming et al. 2015). The theory of structural inertia states that organizations that attempt to adapt too often and too specifically to current conditions can increase their risk of failure in a dynamic environment (Hannan & Freeman 1977, 1984; Haveman 1992; Ruef 2000; Hannan et al. 2003; Barnett & Carroll 2014). Hannan and Freeman (1984) argue that “the worst of all possible worlds is to change structure continually only to find each time upon reorganization that the environment has already shifted to some new configuration that demands yet a different structure”. Structural inertia is therefore viewed as a double-edged sword in organizational ecology, useful in the short-term but ultimately harmful in the long-term by impeding the ability of an organization to adapt to a dramatically-changed environment.

The ability to adapt to change is a central feature of resilience (Folke et al. 2002; Carpenter & Brock 2008), and the concept that adaptation can be detrimental may therefore seem contradictory to social-ecological systems theory. I find support for the importance of adaptive capacity in the PLCA industry, whereby an inability to adapt to the economic environment is likely to effect the sustainability of many financially-motivated PLCAs (Chapters 3 and 6). However, there may be a risk that frequent and specific adaptations in response to fast-changing socioeconomic variables can result in unforeseen but detrimental changes to slow-changing

ecological variables (Chapters 4 and 5), thereby supporting the theory of structural inertia at shorter time periods. The intermediate disturbance hypothesis suggests that local species diversity is maximized when ecological disturbance is neither too rare nor too frequent (Connell 1978). High levels of disturbance are associated with high risk of extinction, while low levels result in a few competitive species establishing dominance (though the concept still receives considerable debate, see for example Fox 2013; Sheil & Burslem 2013). In social-ecological systems, an “intermediate adaptive capacity” concept for organizations would be an interesting hypothesis to explore, where organizational resilience is greatest when adaptation is neither highly frequent, resulting in adaptation to fast-changing socioeconomic variables at the detriment of slower-changing ecological variables, nor very rare, resulting in inert organizations that become unable to meet their objectives in a changed environment.

These ideas are not dissimilar from the principle of the conservation of vulnerability. Vulnerability is the degree to which a system, subsystem, or system component is likely to experience harm due to exposure to a perturbation or stress (Turner et al. 2003). It is proposed that vulnerability in complex systems can be displaced, but not destroyed (Anderies & Norberg 2008). Adaptations that serve to reduce the vulnerability of desirable system resources to natural fluctuations therefore result in an increase in the vulnerability of other, potentially slower-changing system variables (Anderies & Norberg 2008). Given that slower-changing system variables ultimately determine the functioning and resilience of systems (Gunderson & Holling 2002; Norberg & Cumming 2008; Biggs et al. 2012), the theory of the conservation of vulnerability could similarly caution against frequent adaptation in response to fast-changing system variables.

## **7.2 Manager action-outcome feedbacks: pivotal interactions in social-ecological systems**

There are concerns that financially-motivated PLCA managers may be tempted to prioritize profit over biodiversity protection in their management practices, thereby jeopardizing their ecological sustainability (Langholz 1996; Langholz & Lassoie 2001; Cousins et al. 2010; Pasquini et al. 2010b; Miller et al. 2013; Maciejewski & Kerley 2014a, 2014b). Such a concern is not unusual in natural resource management systems; examples of productivity-driven management resulting in ecosystem degradation at longer time scales are ubiquitous (Larkin 1977; Pamo 1998; Carpenter et al. 1999, 2015; Anderies et al. 2002; Folke et al. 2004; Seymour et al. 2010). Commercial PLCAs are interesting social-ecological systems in which to explore the decision-

making that causes these dynamics. Their managers usually have strong conservation objectives (Chapter 3; Langholz 1996; Pasquini et al. 2010b; Stolton et al. 2014), and the potential therefore exists for trade-offs between managing for short-term financial objectives and long-term ecological objectives.

The second objective of this research was to investigate *if, how and why* commercial PLCAs adopt unsustainable ecological management practices. I focused on management related to game (large herbivores) and predators, as natural resources with revenue-generating potential on PLCAs (Chapter 3; Lindsey et al. 2007; Di Minin et al. 2013; Maciejewski & Kerley 2014a), as well as vegetation, since it is a slower-changing system variable that is influenced by large herbivores (Anderies et al. 2002; Seymour et al. 2010). The majority of PLCAs were relatively small (5,400 ha on average), fenced, and comprised of former farmland on which large mammals were extirpated. Supporting a rich diversity and abundance of large mammals therefore required intensive management to stabilize natural ecosystem variation, in the form of game and predator reintroductions, population regulation through hunting, culling or contraception, and actions to enhance and regulate vegetation biomass and water supply (Chapters 4 and 5). Financial objectives were found to influence these ecological management practices. An increased focus on revenue-generation in manager decision-making resulted in increased frequency of actions to stabilize short-term variation in large mammal populations, which led to increased species richness and abundance and thereby increased revenues from ecotourism or hunting. These relationships highlight the high potential for a reinforcing feedback between financially-driven management actions and financially-successful (in the short-term) ecological outcomes on PLCAs. It is therefore important to consider the sustainability of these management practices.

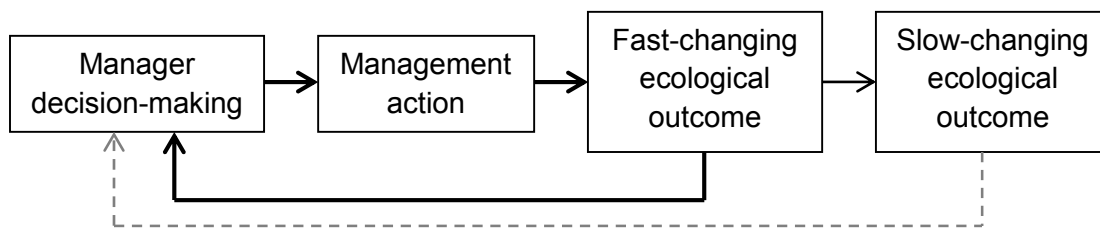
Managing habitats to benefit hunted game species is a global phenomenon, for example tree reduction enhances forage for deer in the United States and burning moorlands in Scotland increases habitat for game birds (Gallo & Pejchar 2016). Despite this global phenomenon, little is known about the conservation implications of these actions on non-target fauna and flora (Gallo & Pejchar 2016). In this thesis I show that increased intensity of management actions that stabilize short-term resource variability corresponded with higher numbers of reintroduced extralimital species, as well as increased rates of game overstocking in the absence of predators (Chapter 4). Over half of PLCAs supporting free-roaming predators were overstocked, corresponding with increased frequency of supplementary feeding and restocking of prey (Chapter 5). These

management actions can have important consequences for the resilience of the managed natural resource system. Management actions that reduce natural ecological variability in the short-term, for example by maintaining large mammals at a constant stocking rate, can increase this variance at longer time scales (Stein 2003) and thereby increase the likelihood of a system being pushed over a threshold and out of its current, desirable state (Carpenter et al. 2015). For example, insecticide spraying in eastern Canada reduced the frequency of boom-and-bust budworm epidemics, resulting in an accumulation of susceptible foliage and making the system less resilient to more intensive and extensive budworm outbreaks (Ludwig et al. 1978). Similarly, the effective suppression of fires in the national parks of the western United States led to the homogenous accumulation of fuel, thereby increasing the system's vulnerability to larger and more widespread fires (Wright & Heinselman 1973). On PLCAs, the maintenance of constant, high stocking rates of game may increase the vulnerability of the vegetation community in times of drought (see for example Anderies et al. 2002; Carpenter et al. 2015), or make the large mammal community less resilient to disease outbreaks (see for example De Vos et al. 2016).

It is generally agreed upon in social-ecological systems thinking that management which aims to reduce natural variability in ecological patterns and processes, such as pest abundance or fire frequency and intensity, reduces system resilience (Wright & Heinselman 1973; Ludwig et al. 1978; Holling 1981; Walker et al. 1981; Holling & Meffe 1996; Anderies et al. 2002; Carpenter et al. 2015). The need to cope with variability, uncertainty and complexity in managing natural resource systems is therefore emphasized, for example through the use of adaptive management, learning, decision-theory and scenario-planning (Holling 1978; Walters 1986; Walters & Holling 1990; Carpenter & Gunderson 2001; Keith et al. 2011; Polasky et al. 2011; Williams 2015). Models have shown that management-monitoring feedbacks can improve the sustainability of resource management in uncertain environments, but lead to “rational routes to collapse” when management decisions are informed by short-term ecosystem trends and when decision support tools don't consider past trends or system thresholds (Peterson et al. 2003; Lindkvist & Norberg 2014). Empirical assessment is lacking, however, of the feedbacks between management actions and outcomes, which emerge due to managers' motivations and reinforce (potentially unsustainable) management practices.

This thesis emphasizes that consideration of these reinforcing action-outcome feedbacks needs to be better integrated into social-ecological systems theory. Management strategies that

achieve short-term financial objectives, despite their negative implications for system resilience over longer time frames, highlight the challenges of managing systems subject to fast- and slow-changing variables (Figs. 1 and 3; Holling & Meffe 1996). Intensive water flow management in the Everglades over the past century, in response to short-term needs and issues such as sugar production, has had a lasting and costly impact on the resilience of the system (Gunderson et al. 1995). Similarly, the majority of PLCA managers focussed on the outcomes of their actions for fast-changing system variables, such as game numbers and revenue, and did not monitor slower-changing system variables such as vegetation, which is shown to be a costly exercise (Chapter 4). They are therefore unlikely to realize the implications of their management actions for slower-changing ecological variables, and continue to implement these seemingly successful strategies. The tight feedbacks between manager decision-making and fast-changing system variables, and the absent or loose feedbacks between manager decision-making and slow-changing systems variables, illustrate how management strategies can become unsustainable, even when conservation is an important objective (Fig. 3).



**Fig. 3.** Relationships between manager decisions, management actions and ecological outcomes in a social-ecological system. Causal relationships are indicated by arrows; bold arrows indicate the tight feedback between managers and fast-changing system variables; the dotted grey arrow indicates a relationship that only exists if managers undertake monitoring of slow-changing biophysical variables.

This thesis further illustrates that facilitating natural ecosystem variability can result in reduced income, impeding the ability of natural resource managers to accumulate the capital necessary to overcome constraints on adaptation, and thus perpetuating their financial vulnerability (Chapter 6). Therefore, the theoretical emphasis on facilitating natural variability in social-ecological systems needs a more practical perspective on the implications of this management approach for achieving managers' objectives (see, for example Little et al. 2016), and the associated implications for system resilience from a financial as well as an ecological perspective.

### **7.3 Governance in private land conservation: theory and practice**

Governance is defined as the exercise of deliberation and decision-making among groups of people who have various sources of authority to act, and may be practiced through a variety of organizational forms (e.g. international unions, national and regional governments, local organizations; Biggs et al. 2012). Polycentric governance refers to a system of governance authorities spanning multiple scales, where each governance unit has independence within a specified geographic area and domain of authority, and each unit may link with others horizontally on common issues and be nested vertically within broader governance units (Biggs et al. 2012). Major challenges in governing social-ecological systems can emerge when the scales of governance are “mismatched” with the scales of the resources being managed, due to inappropriate scales of enforcement and/or a lack of understanding (Cumming et al. 2006; Folke et al. 2007). Therefore, one of the key principles of polycentric governance is to match governance levels to the scale of the problem (Cumming et al. 2006; Folke et al. 2007; Biggs et al. 2012; Guerrero et al. 2015). Polycentric structures are believed to increase modularity and functional redundancy in a governance system, thereby improving its resilience (Biggs et al. 2012). For example, broader levels of governance can step in when lower levels fail to implement effective or appropriate conservation actions (e.g. Newton 2011). In contrast, where institutional failure occurs at the national and international levels, local-level conservation actions can prove imperative (e.g. Paloniemi & Vilja 2009; Lindsey et al. 2014).

At the 5<sup>th</sup> World Parks Conference in Durban in 2003, governance was identified as “central to the conservation of protected areas throughout the world” (World Conservation Union 2003). While protected areas were historically managed by national governments in line with governmental objectives, representing a “top-down” approach to governance, protected area governance structures are now highly diverse, ranging from national and regional government organizations, to nonprofit and for-profit organizations, individuals and communities (refer to Fig. 3 in Chapter 1; Eagles 2009; Leverington et al. 2010). Given the challenges encountered by governments in effectively establishing and enforcing protected areas (Watson et al. 2014), the decentralization of conservation to local, private landowners holds much promise (Langholz & Krug 2004; Stolton et al. 2014). Private land could improve resilience in conservation governance structures by (a) providing conservation capacity where regional and national capacity is low and (b) devolving conservation governance to local landowners that operate at the spatial scale of the



land being conserved. This would reduce the challenge of scale mismatch for example, by incorporating local knowledge on a resource system and how best to manage it. Resilience could also be fostered in the other direction: with regional and national scale governance structures facilitating and regulating local conservation efforts. Many governments have adopted incentive programmes to encourage private land conservation, with positive interaction between landowners and governmental agencies deemed to be an important factor influencing their success (Cooke et al. 2012; Rissman & Sayre 2012; Selinske et al. 2015). Given the findings in this thesis that financial motivations and a lack of ecological monitoring can result in unsustainable management on some PLCAs (Chapters 4 and 5), it could be argued that higher-level governance authorities need to engage more closely with landowners in order to foster sustainable management and/or regulate inappropriate practices.

This is no simple task. A complex mix of state, civil society and private sector organizations are involved in the management and governance of PLCAs (Carter et al. 2008; Pasquini et al. 2010a; McGranahan 2011; Pegas & Castley 2014). Private landowners globally prefer incentive-based, voluntary approaches to conservation on their lands (e.g. Kabii & Horwitz 2006; Mayer & Tikka 2006; Cocklin et al. 2007; Pasquini et al. 2010a), which means governance approaches may be more effective if they rely on cooperation rather than regulation (e.g., Cocklin et al. 2007; Paloniemi & Vilja 2009). PLCA owners in South Africa were found to be hostile towards environmental regulations and distrusting of the governments and agencies that enforced them (Cousins et al. 2010; Pasquini et al. 2010a). In addition, this thesis illustrates that inappropriate policy can have an adverse effect on the sustainability of wildlife management on private land (Chapter 5). While effective conservation on private land holds much promise for improving the resilience of conservation governance systems, careful consideration is required on how to foster appropriate management and continued motivation at this local level of governance.

A complementary option may be to foster knowledge sharing between PLCA managers, as well as between PLCA managers and the managers of other conservation entities, such as regional and national parks. The sharing of information, knowledge, and management strategies between managers provides important opportunities for learning, improved management and monitoring on regional and national protected areas (Maciejewski & Cumming 2015). A recent assessment of the social networks of PLCA managers in South Africa showed that these networks were small and underutilized, and there was a lack of connectivity across institutional levels (private vs.

statutory protected areas) and spatial scales (Maciejewski et al. 2016). The concept of polycentric governance emphasizes the importance of local governance units linking horizontally on common issues, as well as being nested vertically within broader governance units (Biggs et al. 2012). Facilitating sustainable ecological management on PLCAs should therefore include both cross-sector information sharing opportunities, and appropriate engagement with higher-order governance authorities (where ‘appropriate’ engagement provides ecologically accurate information, see Chapter 5, and is cognizant of landowner motivations, see Kusmanoff et al. 2016).

#### **7.4 Practical suggestions and implications**

This thesis emphasizes the importance of ecological monitoring in promoting sustainable natural resource management (Chapter 4). A challenge, however, is the cost of monitoring (Chapters 4 and 6). Many PLCAs do not generate the revenues that would be required to undertake monitoring and still meet their financial objectives (Chapter 3). The industry therefore needs innovative solutions to this challenge. One potential solution is that of volunteer tourism. Volunteer tourism is defined as “tourists who, for various reasons, volunteer in an organized way to undertake holidays that might involve aiding or alleviating the material poverty of some groups in society, the restoration of certain environments, or research into aspects of society or environment” (Wearing 2001, pg 1). Participation in volunteer tourism has grown exponentially over the past several decades. Between 1971 and 2014, the organization Earthwatch involved over 90,000 volunteers in 1400 projects across 120 countries, contributing \$67 million and 11 million hours to scientific fieldwork (McGehee 2014). It is estimated that 10 million people now participate annually in volunteer tourism projects worldwide (McGehee 2014). Several of the PLCA managers that were interviewed for this study had adopted wildlife volunteer programmes, and emphasized their importance. These volunteer programmes serve as self-funded ecological research and monitoring programmes, in that volunteers pay to volunteer. While some studies have raised concerns over the quality of volunteer-collected data (Foster-Smith & Evans 2003), when training is provided and suitable responsibilities are allocated, volunteers can collect high quality data useful for guiding natural resource management (Brightsmith et al. 2008).

This thesis highlights the importance of ecologically-sound policy for wildlife management on private land (Chapter 5). For example, a reassessment of the cheetah minimum area requirements in the Eastern Cape Province’s Certificate of Adequate Enclosure Policy

(Department of Economic Development and Environmental Affairs 2008) is necessary, in light of my finding that this requirement is a significant underestimate (Chapter 5). This finding was brought to the attention of the Department of Economic Development, Environmental Affairs and Tourism in the Eastern Cape Province, who advised in a recent email that “The Biodiversity Technical Committee for the Department agreed yesterday that the minimum area to introduce Cheetah be increased to 2 000 ha. An Amendment was drafted for submission to the General Manager to effect this change. It will also be discussed at the SECSICOM Meeting on Tuesday 26th July” (Email sent to Professor Graham Kerley from Alan Southwood, Environmental Officer: Specialised Production, Department of Economic Development, Environmental Affairs and Tourism; 20 July 2016).

The lack of consensus on what constitutes a “private protected area” and concern over the likely permanence of private protected areas have resulted in private land being largely omitted from international conservation reporting mechanisms, ignored by many governments and excluded from conservation strategies in numerous regions (Stolton et al. 2014). South Africa is relatively well-advanced in its inclusion of private land into its protected area legislation and reporting (Stolton et al. 2014). While only legislated private protected areas contribute to national and provincial protected area targets, the conservation sector recognizes geographic areas that do not fall under the Protected Areas Act, but receive some form of protection by the landowners and are managed at least partly for biodiversity conservation (Stolton et al. 2014). There has been recent debate around expanding the scope of private land conservation types that are included in the national protected area estate, particularly through regional biodiversity stewardship programmes (personal communication, Kerry Purnell, CapeNature, 13 April 2015). Attempts at defining private protected areas to date have focused largely on tenure arrangements and management objectives (Langholz & Lassoie 2001; Langholz & Krug 2004; Carter et al. 2008; Kamal & Brown 2015). My research emphasizes that management objectives are an important consideration and should include consideration of whether or not ecological monitoring is undertaken. Furthermore, even if a PLCA is subject to ecologically-sound management, if it is not able to achieve its financial objectives in the long-term it may not be sustainable from a financial perspective. Financial sustainability is therefore an important consideration when including private land into national protected area estates, given the assumption that these estates provide conservation in perpetuity.

## 7.5 Reflections on the research approach

This study was based largely on an empirical dataset, collected through visits to PLCAs and engagement with their managers. For some of the PLCA characteristics under consideration in this study, this dataset was representative of one year of information. For example, I was able to acquire only a single year of financial data. Longer-term datasets proved challenging to obtain either because managers were reluctant to share substantial financial datasets or because this information had not been appropriately archived and was therefore unavailable. Interpretation of the drivers of profitability in this thesis is therefore specific to a single year, and likely to fluctuate over time with changing tourist preferences, global economies, fuel prices, etc. While my findings are in support of previous studies and therefore appear to be an accurate representation of general trends in the industry, I emphasize in Chapters 3 and 6 that additional years of financial data would be beneficial in confirming these patterns.

Given the single year of data, many of the analyses in this thesis make use of a “space for time” substitution. A large sample size enabled me to undertake quantitative statistical analyses, such as cluster analyses (Chapter 3), structural equation models (Chapter 4) and linear models (Chapter 5), in order to test predictions. Emergent relationships were interpreted *dynamically*, for example “an increase in management intensity led to an increase in game abundance” (Chapter 4) or “higher lion densities led to higher revenues” (Chapter 5), although the relationships themselves were observed statically in time. The absence of time series data limited my ability to quantify empirically the likely feedbacks arising from these relationships. In Chapter 3, for example, patterns of financial objectives and profitability suggest that PLCA managers may be constrained in their ability to adapt their business model to changing economic conditions, but I was unable to assess this empirically. Similarly, Chapter 4 highlights relationships between managers’ use of revenue to inform management, management actions, and ecological and financial outcomes. There is, therefore, the strong likelihood that financial outcomes influence future management decisions, but I was unable to test this empirically. By developing a mechanistic PLCA model with which to test hypothesized drivers of observed relationships on PLCAs (Chapter 6), I was able to overcome the static nature of the data to some extent. For example, this model enabled me assess dynamically whether PLCA characteristic incompatibilities limited business model adaptation, as predicted in Chapter 3.

Many of my findings provide insight into the likely sustainability of the PLCA industry. For example, overstocking is likely to erode ecological sustainability, while ecological monitoring appears to promote ecological sustainability. Similarly, PLCAs that do not have financial objectives or are able to achieve their financial objectives are likely to be more sustainable than those that are unable to meet their financial objectives. I was not able to explicitly measure PLCA sustainability, however, in the absence of time-series data. I lacked detailed ecological data that would have enabled a more direct assessment of ecological management practices, such as vegetation composition and quality and large mammal body condition and population trends. Data on failed PLCAs would similarly have enabled a more direct assessment of drivers of sustainability. In a relatively short-term study, such as a three year PhD, there is a trade-off in many cases between collecting a large dataset and a detailed dataset. Visiting 72 PLCAs enabled me to undertake insightful quantitative analyses, from which I could contribute to social-ecological system theory and provide grounded generalizations about the PLCA industry, but this was offset against collecting more detailed site-specific data.

## **7.6 Future research directions**

Path dependence is a concept that has been applied across several fields, including economics (Arthur 1994), ecology (Cumming & George 2009), social-ecological systems (Grove 2009; Mendez et al. 2012), and organizational science (Sydow et al. 2009; Heine & Rindfleisch 2013). It is a mechanism inherent within complex systems subject to multiple stable states. These states are separated by a threshold in one or more system property (Holling 1973; Gunderson 2000; Folke et al. 2004). Seemingly small initial differences in the properties of two systems can position them on opposite sides of this threshold between states. These small initial differences can become magnified over time as each system follows the self-reinforcing path inherent to its state (Holling 1973; Gunderson 2000; Folke et al. 2004). In a variable environment, long-term success is dependent on the capacity to adapt through change (Holling 2001). Path dependency can erode system resilience if it impedes this adaptive capacity, causing a system to become trapped in an undesirable state (Carpenter & Brock 2008).

While the concept of path dependence is not new to social-ecological systems studies, particularly in understanding the behaviour of institutions (Allison & Hobbs 2004; Mwangi 2006; Mendez et al. 2012), this study illustrates how this concept, together with others that are unique to

the organizational sciences (e.g. Fig. 2), can be useful in understanding *organizational* behaviour in social-ecological systems. The role of organizations, as opposed to institutions, in maintaining social-ecological systems in desirable or undesirable states has received minimal attention in social-ecological systems research. Organizations are likely to be a key determinant of resilience in some systems, as highlighted by this study. Future social-ecological systems research should therefore benefit from a more explicit consideration of organizational patterns and processes as system drivers, as described in section 7.1.

There is persistent debate in the business literature on the causes of organizational success or failure. Classical industrial organizational studies and organizational ecology assume that the environment is the primary driver of success or failure, and that managers are constrained by inert organizations that limit their strategic choices (Mellahi & Wilkinson 2004). In contrast, organizational psychology argues that managers are the principal decision makers of the organization and, consequently, their actions and perceptions are the fundamental cause of organizational performance (Mellahi & Wilkinson 2004). The relative selective pressures of internal agency and the external environment have been subject to similar debate in institutional studies, where this is an issue of significance in the design of effective institutions for governing natural resources (Hardin 1968; Ostrom 1990; Dietz et al. 2003; Cumming 2016b). This thesis illustrates how internal agency and the external environment *interact* to drive sustainability in a social-ecological system. A manager makes initial strategic decisions, such as where and how much land to purchase and how to generate revenue from his/her natural resources. The external environment sets constraints on this system (such as the combinations of characteristics that are viable and how much revenue they can generate; Chapter 3). Notably, the manager has the ability to alter the organization's developmental trajectory within those constraints, dependent on objectives, management strategies and monitoring focus (Chapters 4, 5 and 6). Future organizational research and social-ecological systems research alike could therefore benefit from a less polarized perspective on internal agency and the external environment.

Future social-ecological systems research should also benefit from a more explicit consideration of management action-outcome feedbacks in driving system dynamics, as described in section 7.2. It is certainly useful to propose ways to facilitate sustainable natural resource management in an uncertain environment, such as through adaptive management and co-learning (Holling 1978; Walters 1986; Walters & Holling 1990; Carpenter & Gunderson 2001). However,

more emphasis needs to be placed on understanding current decision-making behaviours and how these function dynamically, resulting in feedbacks between decision-making, actions, and outcomes (e.g. Fig. 3). Research in behavioural economics, psychology, and behavioural decision theory has shown that people are subject to a range of biases in their perceptions and judgments, many of which are likely to be applicable to natural resource managers (Table 1; Iftekhhar & Pannell 2015). There is a growing field of behavioural experimentation in natural resource management aimed at understanding manager decision-making as well as learning and cooperation, particularly in common pool resource systems (McAllister et al. 2006; Anderies et al. 2011; Cardenas et al. 2013; Yu et al. 2016). Our growing understanding of manager behaviour paves the way for exciting new empirical studies on how and why natural resource managers influence the dynamics and resilience of a diverse range of social-ecological systems.

**Table 1.** Behavioural biases with potential to influence natural resource manager decision-making (Iftekhhar & Pannell 2015)

<b>Bias</b>	<b>Description</b>
Action bias	Tendency to take action even when it is better to delay action
Framing effect	Tendency to respond differently to alternatively worded but objectively equivalent descriptions of the same item
Reference-point bias	Tendency to overemphasize a predetermined benchmark for a variable when estimating the level of that variable
Availability heuristic	Tendency to give more weights to events that can be recalled more easily
Planning fallacy	Making judgments about a planned activity that are systematically overoptimistic, including underestimating project completion time, underestimating costs, or overestimating benefits
“Satisficing rule”	Tendency to stop searching for a better decision once a decision that seems sufficiently good is identified
Loss aversion	Tendency to value losses more highly than similar gains
Reliance on limited information	Tendency to use a subset of information even when full set of information is available
Limited reliance on systematic learning	Tendency to use information from past successful efforts rather than using information from both successful and failed efforts

The role of diversity in maintaining resilience has received considerable attention across a broad range of fields (Stirling 2007). In the context of a social-ecological system, diversity can be considered at the level of genes, species, landscapes, cultures, livelihoods, and governance institutions. It therefore encompasses biodiversity, spatial heterogeneity, livelihood strategies, and institutional diversity (Biggs et al. 2012). Response diversity, or “functional redundancy”, is diversity in response to disturbances among species or actors that contribute the same function within a system (Elmqvist et al. 2003; Walker et al. 2006). There is consensus from a variety of

disciplines that diversity and redundancy are important for resilience because they provide options for responding to change and disturbance (Folke et al. 2002, 2005; Stirling 2007; Chapin & Kofinas 2009; Ostrom 2009a; Biggs et al. 2012). For example, people who develop a diverse set of activities to generate revenue from a natural resource system (e.g., fishing and ecotourism) build resilience in their livelihoods by creating options for rebalancing these activities in response to market or environmental changes (Ellis 2000; Biggs et al. 2012).

While much attention has been placed on the importance of diversity and redundancy in promoting resilience in social-ecological systems, this thesis makes a novel theoretical contribution to understanding the processes that *create* (or eliminate) diversity in social-ecological systems, thereby highlighting an interesting avenue for further research. Resilience theory tells us that it would be prudent for PLCA managers to diversify the activities offered on their PLCAs, such as hunting, live game sales and ecotourism, targeting both international and local markets. These activities and markets are likely to respond to changes and disturbances in different ways, thereby reducing financial vulnerability. In reality, however, these activities are incompatible in many cases, with options for diversity thus constrained (Chapter 3). This suggests that an understanding of resilience in social-ecological systems would benefit from an increased focus on the mechanisms that give rise to diversity, or the lack thereof. This study illustrates how organizational incompatibilities in spatial, ecological and socioeconomic characteristics constrain options for generating revenue from a privately managed natural resource system. Can the concept of social-ecological incompatibilities explain patterns of diversity in the livelihoods of individuals operating in a common pool resource system, or patterns of diversity in the functioning of large-scale conservation NGOs? And can we use commonalities and differences in these patterns between social-ecological systems to develop and test theories for the types of incompatibilities that emerge and the ways in which they influence diversity?

This thesis draws the somewhat unusual conclusion that facilitating diversity in certain ecological attributes (such as large mammals) may not always be a good thing, if it arises as a result of management that reduces natural variability in the ecosystem (Chapter 4). Ecotourist and hunter preferences drive managers to enhance large mammal diversity on their PLCAs, but space limitations and the introduction of extralimital species necessitate intensive management to ensure stable water and food provision. These social-ecological systems are therefore subject to a trade-off between managing for diversity and variability. Diversity and variability are system attributes



that are both believed to contribute to resilience, and are usually viewed as positively related (Holling & Meffe 1996; Carpenter et al. 2015). In many natural resource systems, managers reduce ecological diversity in order to reduce natural resource variability, for example farmers replace diverse flora and fauna with monocultures or livestock to stabilize variability in food yield (Holling & Meffe 1996). However, this study illustrates that there are situations when the variability and diversity of certain ecological attributes is not linearly and positively related, raising interesting questions regarding (a) what other social-ecological systems may mirror this relationship and (b) where resilience is maximized on the spectrum from diversity to variability in such systems. Managing habitats to benefit hunted species is a global activity that has been implemented for centuries (Gallo & Pejchar 2016), and may therefore be a widespread example of managing natural variability to promote diversity in target species. Ecological diversity is important in the provision of cultural ecosystem services, and the trade-off between ecological diversity and variability may therefore arise in other social-ecological systems that are managed with the aim of generating revenue from cultural ecosystem service provision (Fuller et al. 2007; Schaich et al. 2010; Naidoo et al. 2011; De Vos et al. 2015).

Broadly defined, ecosystems services are “the benefits people obtain from ecosystems” (Millenium Ecosystem Assessment 2005), or “the contributions that ecosystems make to human well-being” (Haines-Young & Potschin 2012) and include provisioning, regulation and maintenance, and cultural services (Millenium Ecosystem Assessment 2005; Sukhdev et al. 2010; Haines-Young & Potschin 2012). An ecosystem services perspective would be useful in assessing the mechanisms behind the observed predictors of revenue and profitability on PLCAs (Chapters 3, 4 and 5). By asking PLCA tourists and/or hunters why they chose to visit a given PLCA, we could gain a better understanding of how and why affordability, accessibility, infrastructure, activities and ecological attributes influence the incomes generated by PLCAs (Chapter 3). Given the high level of correlation between predictors of profitability on PLCAs (such as between size, game numbers and price), an assessment of why people visit PLCAs would allow for a more specific differentiation of the relative strength of these predictors.

A cultural ecosystem services study of visitors to South Africa’s National Parks illustrates that different parks attract people seeking different bundles of ecosystem services, such as “natural history”, “recreation”, “sense of place”, “safari experiences” and “outdoor lifestyle” (Ament et al. 2016). Similar to the finding that distinct business models are differentiated by incompatibilities

in socioeconomic and ecological attributes (Chapter 3), Ament and colleagues found that bundles of services are differentiated by trade-offs between certain service requirements, and the likely availability of particular service bundles in specific ecosystems. However, the *drivers* of different ecosystem service bundles were not assessed quantitatively. It would be interesting to assess whether bundles of cultural ecosystem services emerge on PLCAs, and if these are driven by the different business models. For example, I would predict big game business models to be associated with a “safari experience” ecosystem service bundle. In contrast, the budget business model, which lacks game and associated safari activities, and attracts local visitors, may be better associated with “sense of place” and “natural history”. Hunting PLCAs may represent more physically-active ecosystem services, such as “recreation” and “outdoor lifestyle”. In particular, it would be interesting to see if there are outliers to the emergent patterns (for example, PLCAs with a specific business model who attract people seeking ecosystem services generally associated with an alternative business model), and how this affects profitability. There was variability in incomes within PLCA business models (Chapter 3), and an ecosystem services perspective may provide some insight into why this is the case. For example, a PLCA that is characterized by a big game business model usually associated with “safari experiences”, who attracts people seeking “outdoor lifestyle” may be targeting the wrong market and/or charging inappropriate prices.

A recent study assessed “bright spots” among the world’s coral reefs, which are defined as places where ecosystems are in substantially better condition than expected, given the environmental conditions and socioeconomic drivers that they are exposed to (Cinner et al. 2016). It was proposed that these outliers could provide insight into the factors (independent from the environmental and socioeconomic factors used to detect outliers) that enable a given coral reef to perform better than expected. Cinner and colleagues found that coral reef bright spots were characterized by strong sociocultural institutions, high levels of local engagement in management, high dependence on marine resources, and beneficial environmental conditions (Cinner et al. 2016). It would be interesting to undertake a similar study for PLCAs, identifying outliers in management and profitability. For example, are there PLCAs that generate greater incomes than expected given their biophysical and socioeconomic characteristics? Are their PLCAs that generate a profit, undertake ecological monitoring and manage their ecosystems sustainably, and, if so, why? On a practical level, such an investigation would enable us to explore potential ways to alleviate the trade-off, observed in this study, between managing for short-term financial versus

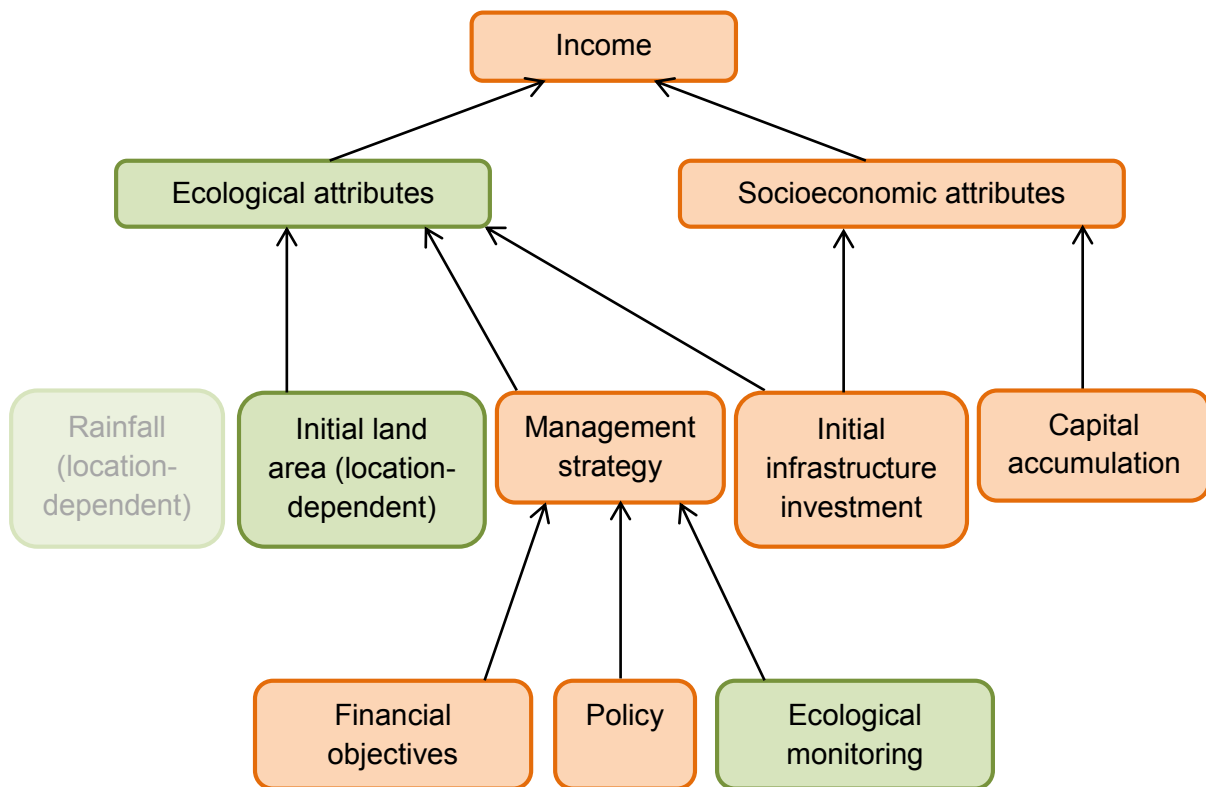
long-term ecological objectives. On a more theoretical level, such an investigation could provide insight into the organizational attributes and behaviours that promote sustainable ecological management.

Private land conservation is regarded as a “cost-effective” conservation tool for governments, and there is a substantial body of literature assessing the cost-effectiveness to governments around the world of incentivizing conservation on private land, and the costs of establishing and maintaining statutory protected areas (Bruner et al. 2004; Swift et al. 2004; Mayer & Tikka 2006; Naidoo et al. 2006; Crossman & Bryan 2009; Von Hase et al. 2010; Adams et al. 2012). In this thesis I illustrate that there is a trade-off between optimizing revenues and sustainably managing large mammals (Chapters 4 and 5). An interesting avenue of future research would be to adopt an ecological economics approach, and assess the opportunity cost of sustainable management (i.e. potential revenue minus revenue generated under sustainable management). This cost could be compared with the cost to governments of establishing statutory protected areas. I would predict that, given the significant costs of establishing and maintaining protected areas (Bruner et al. 2004), there would be economic justification for the provision of government-funded financial incentives to PLCA managers to undertake sustainable ecological management.

## **7.7 Conclusion**

Insight into the ecological and economic sustainability of the commercial PLCA industry can be gained through cognizance that PLCAs emerge from multi-scale, social-ecological interactions. Figure 4 illustrates the drivers of PLCA ecological management and profitability, which were assessed in this thesis. Financial objectives, ecological monitoring (or the lack thereof), and regional policy requirements influence the management strategy that a given PLCA manager adopts. The adopted management strategy, together with the manager’s initial decisions regarding land and infrastructural investments and the capital that the PLCA accumulates over time, influence the PLCA’s ecological and socioeconomic attributes and thereby its income-generating potential. Feedbacks between a manager’s actions and their outcomes can reinforce ecologically sustainable or unsustainable management practices, depending on whether ecological monitoring or financial objectives inform management. Feedbacks between ecological and socioeconomic attributes and PLCA income, in turn, can reinforce financially sustainable or

unsustainable business strategies, depending on whether accumulated capital is sufficient to overcome organizational constraints on adaptation.



**Fig. 4.** Logic tree illustrating the hypothesized drivers of Private Land Conservation Area profitability and management, tested in this thesis (Chapters 3 to 6). Social drivers are illustrated in orange and ecological/biophysical drivers are illustrated in green. Rainfall is shown as a transparent box since it did not emerge as a significant driver.

The decisions made by natural resource managers can set up self-reinforcing management regimes and organizations, with the potential to build or break down resilience in the systems that they manage. Focusing on natural resource managers has enabled me to broaden current perspectives on organizational behaviour, management action-outcome feedbacks, governance, diversity and variability, and the relative selective pressures of internal agency versus the external environment in social-ecological systems. I conclude that natural resource managers are dynamic actors in social-ecological systems, and emphasis should be placed on the role that they can play in building resilient and sustainable societies.

## REFERENCES

- Abel N, D. H. M. Cumming, and J. M. Anderies. 2006. Collapse and reorganization in social-ecological systems: Questions, some ideas, and policy implications. *Ecology and Society* **11**:17.
- Absa Group Economic Research. 2003. Game Ranch Profitability in Southern Africa, 3rd edition. The SA Financial Sector Forum, Rivonia, South Africa.
- Adams, V. M., R. L. Pressey, and N. Stoeckl. 2012. Estimating land and conservation management costs: The first step in designing a stewardship program for the Northern Territory. *Biological Conservation* **148**:44–53.
- Adams, W. M., and J. Hutton. 2007. People, Parks and Poverty: Political Ecology and Biodiversity Conservation. *Conservation and Society* **5**:147–183.
- Adger, W. N. 2006. Vulnerability. *Global Environmental Change* **16**:268–281.
- AfriGIS. 2013. AfriGIS Cadastre.
- Allen, C. R., G. S. Cumming, A. S. Garmestani, D. Phillip, and B. H. Walker. 2011. Managing for resilience. *Wildlife Biology* **17**:337–349.
- Allen, C. R., and L. H. Gunderson. 2011. Pathology and failure in the design and implementation of adaptive management. *Journal of Environmental Management* **92**:1379–1384.
- Allison, H. E., and R. J. Hobbs. 2004. Resilience, adaptive capacity, and the “lock-in trap” of the Western Australian agricultural region. *Ecology and Society* **9**:3.
- Ament, J. M., C. A. Moore, M. Herbst, and G. S. Cumming. 2016. Cultural ecosystem services in protected areas: understanding bundles, trade-offs and synergies. *Conservation Letters*, In press.
- Anderies, J. M. 2015. Managing variance: Key policy challenges for the Anthropocene. *Proceedings of the National Academy of Sciences of the United States of America* **112**:14402–14403.
- Anderies, J. M., A. A. Rodriguez, M. A. Janssen, and O. Cifdaloz. 2007. Panaceas, uncertainty, and the robust control framework in sustainability science. *Proceedings of the National Academy of Sciences of the United States of America* **104**:15194–15199.
- Anderies JM, and M. A. Janssen. 2016. Institutions and the performance of Coupled Infrastructure Systems. *International Journal of the Commons* **10**:1–10.

- Anderies, J. M., M. A. Janssen, F. Bousquet, J. C. Cardenas, D. Castillo, M. C. Lopez, R. Tobias, B. Vollan, and A. Wutich. 2011. The challenge of understanding decisions in experimental studies of common pool resource governance. *Ecological Economics* **70**:1571–1579.
- Anderies, J. M., M. A. Janssen, and E. Ostrom. 2004. A Framework to Analyze the Robustness of Social-ecological Systems from an Institutional Perspective. *Ecology and Society* **9**:18.
- Anderies, J. M., M. A. Janssen, and B. H. Walker. 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. *Ecosystems* **5**:23–44.
- Anderies, J. M., and J. Norberg. 2008. Theoretical challenges: Information processing and navigation in social-ecological systems. Pages 155–179 in J. Norberg and G. S. Cumming, editors. *Complexity theory for a sustainable future*. Columbia University Press, New York.
- Armsworth, P. R. et al. 2015. Are conservation organizations configured for effective adaptation to global change? *Frontiers in Ecology and the Environment* **13**:163–169.
- Arthur, W. B. 1994. *Increasing returns and path dependence in the economy*. University of Michigan Press, Michigan.
- Ban, N. C. et al. 2013. A social-ecological approach to conservation planning: Embedding social considerations. *Frontiers in Ecology and the Environment* **11**:194–202.
- Baral, N. 2013. What makes grassroots conservation organizations resilient? An empirical analysis of diversity, organizational memory, and the number of leaders. *Environmental Management* **51**:738–749.
- Barnes, J. I. 2001. Economic returns and allocation of resources in the wildlife sector of Botswana. *South African Journal of Wildlife Research* **31**:141–153.
- Barnes, J. I., and J. L. de Jager. 1996. Economic and financial incentives for wildlife use on private lands in Namibia and the implications for policy. *South African Journal of Wildlife Research* **26**:37–46.
- Barnett, W. P., and G. R. Carroll. 2014. Modeling Internal Organizational Change. *Annual Review of Sociology* **21**:217–236.
- Barnosky, A. D. et al. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* **471**:51–57.
- Barrett, C. B., K. Brandon, C. Gibson, and H. Gjertsen. 2001. Conserving Tropical Biodiversity amid Weak Institutions. *BioScience* **51**:497–502.
- Baum, J. 2016. *The Influence of Location on the Structure and Functioning of Private Land*

- Conservation Networks in the Western Cape Province of South Africa. PhD thesis, University of Cape Town, Cape Town.
- Baum, J. A. 1999. Organizational ecology. Pages 71–108 in S. R. Clegg, S. Clegg, and C. Hardy, editors. *Studying Organization: Theory and Method*. Sage Publications, Inc.
- Bayliss, J., M. Schaafsma, A. Balmford, N. D. Burgess, J. M. H. Green, S. S. Madoffe, S. Okayasu, K. S. H. Peh, P. J. Platts, and D. W. Yu. 2014. The current and future value of nature-based tourism in the Eastern Arc Mountains of Tanzania. *Ecosystem Services* **8**:75–83.
- Beedell, J. D. C., and T. Rehman. 1999. Explaining farmers' conservation behaviour: Why do farmers behave the way they do? *Journal of Environmental Management* **57**:165–176.
- Berkes, F. et al. 2006. Globalization, roving bandits, and marine resources. *Science* **311**:1557–1558.
- Berkes, F. 2007. Community-based conservation in a globalized world. *Proceedings of the National Academy of Sciences of the United States of America* **104**:15188–15193.
- Berkes, F., J. Colding, and C. Folke. 2003. *Navigating social-ecological systems: building resilience for complexity and change*. Cambridge University Press, Cambridge.
- Berkes, F., C. Folke, and J. Colding. 2000. *Linking social and ecological systems: management practices and social mechanisms for building resilience*. Cambridge University Press, Cambridge.
- Biggs, R. et al. 2012. Toward principles for enhancing the resilience of ecosystem services. *Annual Review of Environment and Resources* **37**:421–448.
- Bissett, C., and R. T. F. Bernard. 2007. Habitat selection and feeding ecology of the cheetah (*Acinonyx jubatus*) in thicket vegetation: is the cheetah a savanna specialist? *Journal of Zoology, London* **271**:310–317.
- Blaikie, P., and H. Brookfield. 1987. *Land Degradation and Society*. Routledge, New York.
- Bode, M., W. Probert, W. R. Turner, K. A. Wilson, and O. Venter. 2011. Conservation planning with multiple organizations and objectives. *Conservation Biology* **25**:295–304.
- Bond, I., B. Child, D. de la Harpe, B. Jones, J. Barnes, and H. Anderson. 2004. Private Land Contribution to Conservation in South Africa. Pages 29–62 in B. Child, editor. *Parks in Transition: Biodiversity, Rural Development, and the Bottom Line*. Earthscan, New York.
- Borcard, D., F. Gillet, and P. Legendre. 2011. *Numerical Ecology with R*. Springer, New York.

- Bothma, J. du P. 2002. Game ranch management. Van Schaik Publishers, Pretoria.
- Brightsmith, D. J., A. Stronza, and K. Holle. 2008. Ecotourism, conservation biology, and volunteer tourism: A mutually beneficial triumvirate. *Biological Conservation* **141**:2832–2842.
- Brunckhorst, D. J. 2002. Institutions to sustain ecological and social systems. *Ecological Management and Restoration* **3**:108–116.
- Bruner, A. G., R. E. Gullison, R. E. Rice, and G. A. B. da Fonseca. 2001. Effectiveness of parks in protecting tropical biodiversity. *Science* **291**:125–128.
- Bruner, A., R. Gullison, and A. Balmford. 2004. Financial costs and shortfalls of managing and expanding protected-area systems in developing countries. *BioScience* **54**:1119–1126.
- Butchart, S. H. M. et al. 2010. Global biodiversity: indicators of recent declines. *Science* **328**:1164–1168.
- Cadman, M. 2010. Biodiversity for Development: South Africa's landscape approach to conserving biodiversity and promoting ecosystem resilience. South African National Biodiversity Institute, Pretoria.
- Cape Nature Biodiversity Support Services. 2014. Policy on Fencing and Enclosure of Game, Predators and Dangerous Animals in the Western Cape Province. Stellenbosch.
- Cardenas, J., M. Janssen, and F. Bousquet. 2013. Dynamics of Rules and Resources: Three New Field Experiments on Water, Forests and Fisheries. Pages 319–345 in J. A. List and M. K. Price, editors. *Handbook on Experimental Economics and the Environment*. Edward Elgar, Cheltenham.
- Carpenter, S. R., and W. A. Brock. 2008. Adaptive Capacity and Traps. *Ecology and Society* **13**:40.
- Carpenter, S. R., W. A. Brock, C. Folke, E. H. van Nes, and M. Scheffer. 2015. Allowing variance may enlarge the safe operating space for exploited ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **112**:14384–14389.
- Carpenter, S. R., and L. H. Gunderson. 2001. Coping with Collapse: Ecological and Social Dynamics in Ecosystem Management. *BioScience* **51**:451–457.
- Carpenter, S. R., D. Ludwig, and W. A. Brock. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecological Applications* **9**:751–771.
- Carpenter, S., B. Walker, J. M. Anderies, and N. Abel. 2001. From Metaphor to Measurement:



- Resilience of What to What? Ecosystems **4**:765–781.
- Carter, E., W. M. Adams, and J. Hutton. 2008. Private protected areas: management regimes, tenure arrangements and protected area categorization in East Africa. *Oryx* **42**:177–186.
- Carter, M. R., and C. B. Barrett. 2006. The economics of poverty traps and persistent poverty: An asset-based approach. *Journal of Development Studies* **42**:178–199.
- Cash, D. W., and S. C. Moser. 2000. Linking global and local scales: dynamic assessment and management processes. *Global Environmental Change* **10**:109–120.
- Castley, J. G. 2010. Southern and East Africa. Pages 145– 175 in R. Buckley, editor. Conservation tourism. CAB International, Wallingford.
- Castley, J. G., A. F. Boshoff, and G. I. H. Kerley. 2001. Compromising South Africa's natural biodiversity - inappropriate herbivore introductions: commentary. *South African Journal of Science* **97**:344–348.
- Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Son, New York.
- Caughley, G., and C. Krebs. 1983. Are big animals simply little mammals writ large? *Oecologia* **59**:7–17.
- CBD. 2011. COP 10 Decision X/2: Strategic Plan for Biodiversity 2011–2020. Available from [www.cbd.int/decision/cop/?id=12268](http://www.cbd.int/decision/cop/?id=12268) (accessed August 18, 2016).
- Chape, S., J. Harrison, M. Spalding, and I. Lysenko. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **360**:443–455.
- Chapin, F. S., and G. P. Kofinas. 2009. Sustaining Livelihoods and Human Well-Being during Social–Ecological Change. Pages 55–75 in F. S. Chapin, G. P. Kofinas, and C. Folke, editors. *Principles of Ecosystem Stewardship: Resilience-Based Natural Resource Management in a Changing World*. Springer Science & Business Media.
- Child, B. 2004. *Parks in Transition. Biodiversity, Rural Development and the Bottom Line*. Earthscan, New York.
- Child, B. A., J. Musengezi, G. D. Parent, and G. F. T. Child. 2012. The economics and institutional economics of wildlife on private land in Africa. *Pastoralism: Research, Policy and Practice* **2**:18.
- Child, M. F., M. J. S. Peel, I. P. J. Smit, and W. J. Sutherland. 2013. Quantifying the effects of

- diverse private protected area management systems on ecosystem properties in a savannah biome, South Africa. *Oryx* **47**:29–40.
- Cinner, J. E. et al. 2016. Bright spots among the world's coral reefs. *Nature* **535**:416–419.
- Cinner, J. E., N. A. J. Graham, C. Huchery, and M. A. Macneil. 2013. Global Effects of Local Human Population Density and Distance to Markets on the Condition of Coral Reef Fisheries. *Conservation Biology* **27**:453–458.
- Clark, C. W. 1976. *Mathematical Bioeconomics, the optimal control of renewable resources*. John Wiley, New York.
- Clark, W. C., N. M. Dickson, D. W. Cash, F. Alcock, N. Eckley, D. H. Guston, J. Jäger, and R. B. Mitchell. 2003. Sustainability science: the emerging research program. *Proceedings of the National Academy of Sciences of the United States of America* **100**:8086–8091.
- Clarke, J. N., and D. C. McCool. 1996. *Staking out the terrain: Power and performance among natural resource agencies*, 2nd edition. State University of New York Press, Albany.
- Cochrane, M. A., and W. F. Laurance. 2002. Fire as a large-scale edge effect in Amazonian forests. *Journal of Tropical Ecology* **18**:311–325.
- Cocklin, C., N. Mautner, and J. Dibden. 2007. Public policy, private landholders: Perspectives on policy mechanisms for sustainable land management. *Journal of Environmental Management* **85**:986–998.
- Coe, M. J., D. H. Cumming, and J. Phillipson. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* **22**:341–354.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. *Science* **199**:1302–1310.
- Cooke, B., W. T. Langford, and A. Gordon. 2012. Social context and the role of collaborative policy making for private land conservation. *Journal of Environmental Planning and Management* **55**:37–41.
- Coomes, O. T., Y. Takasaki, and J. M. Rhemtulla. 2011. Land-use poverty traps identified in shifting cultivation systems shape long-term tropical forest cover. *Proceedings of the National Academy of Sciences of the United States of America* **108**:13925–13930.
- Costanza, R. 1989. What is ecological economics? *Ecological Economics* **1**:1–7.
- Costanza, R. et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* **387**:253–260.

- Cousins, J. A., J. P. Sadler, and J. Evans. 2010. The challenge of regulating private wildlife ranches for conservation in South Africa. *Ecology and Society* **15**:23.
- Cousins, J., J. Sadler, and J. Evans. 2008. Exploring the role of private wildlife ranching as a conservation tool in South Africa: stakeholder perspectives. *Ecology and Society* **13**:43.
- Cox, M., S. Villamayor-Tomas, G. Epstein, L. Evans, N. C. Ban, F. Fleischman, M. Nenadovic, and G. Garcia-lopez. 2016. Synthesizing theories of natural resource management and governance. *Global Environmental Change* **39**:45–56.
- Creel, S. et al. 2013. Conserving large populations of lions - the argument for fences has holes. *Ecology Letters* **16**:1413.
- Creel, S., and N. M. Creel. 1997. Lion density and population structure in the Selous Game Reserve: Evaluation of hunting quotas and offtake. *African Journal of Ecology* **35**:83–93.
- Creswell, J. W., E. Ostrom, D. Diniz, A. Terra, M. G. Schapiro, M. D. McGinnis, D. M. Trubek, D. R. Coutinho, and M. G. Schapiro. 2014. An introduction to IAD and the language of the Ostrom workshop: a simple guide to a complex framework. *Policy Studies Journal* **39**:7–27.
- Crossman, N. D., and B. A. Bryan. 2009. Identifying cost-effective hotspots for restoring natural capital and enhancing landscape multifunctionality. *Ecological Economics* **68**:654–668.
- Cumming, D. et al. 1997. Elephants, woodlands and biodiversity in Southern Africa. *South African Journal of Science* **93**:231–236.
- Cumming, D. H. M., and G. S. Cumming. 2003. Ungulate community structure and ecological processes: body size, hoof area and trampling in African savannas. *Oecologia* **134**:560–568.
- Cumming, G., D. Cumming, and C. Redman. 2006. Scale mismatches in social-ecological systems: causes, consequences, and solutions. *Ecology and Society* **11**:14.
- Cumming, G. S. 2011. *Spatial resilience in social-ecological systems*. Springer, London.
- Cumming, G. S. 2014. Theoretical Frameworks for the Analysis of Social-Ecological Systems. Pages 3–24 *Social-Ecological Systems in Transition*, Global Environmental Studies. Springer, Japan.
- Cumming, G. S. et al. 2015. Understanding protected area resilience: a multi-scale, social-ecological approach. *Ecological Applications* **25**:299–319.
- Cumming, G. S. 2016a. The relevance and resilience of protected areas in the Anthropocene. *Anthropocene* **13**:46–56.
- Cumming, G. S. 2016b. Heterarchies: Reconciling Networks and Hierarchies. *Trends in Ecology*

- & Evolution **31**:622–632.
- Cumming, G. S., and A. George. 2009. Historical influences dominate the composition of regenerating plant communities in abandoned citrus groves in north-central Florida. *Landscape Ecology* **24**:957–970.
- Daily, G. 1997. *Nature's Services: Societal Dependence on Natural Ecosystems*. Island Press, Washington DC.
- Darnhofer, I., W. Schneeberger, and B. Freyer. 2005. Converting or not converting to organic farming in Austria: Farmer types and their rationale. *Agriculture and Human Values* **22**:39–52.
- de Snoo, G. R. et al. 2013. Toward effective nature conservation on farmland: Making farmers matter. *Conservation Letters* **6**:66–72.
- De Vos, A., G. S. Cumming, D. H. M. Cumming, J. Ament, J. Baum, H. S. Clements, J. D. Grewar, K. Maciejewski, and C. Moore. 2016. Pathogens, disease, and the social-ecological resilience of protected areas. *Ecology and Society* **21**:20.
- De Vos, A., G. S. Cumming, C. A. Moore, and K. Maciejewski. 2015. Understanding the role of ecotourism attributes for the economic sustainability of protected areas. *Ecosphere* **7**:e01207.
- Defries, R., A. Hansen, B. L. Turner, R. Reid, and J. Liu. 2007. Land use change around protected areas: Management to balance human needs and ecological function. *Ecological Applications* **17**:1031–1038.
- Department of Economic Development and Environmental Affairs. 2008. *Operational Guidelines of the Chief Directorate of Environmental Affairs 2008: Certificate of Adequate Enclosure & Dangerous Game Fencing Specifications*. Bhisho.
- Department of Environmental Affairs. 2016. South African Protected Areas Database. Available from <http://egis.environment.gov.za/sapad.aspx?m=64>.
- Department of Environmental Affairs and Tourism. 2008. *National Norms and Standards Schedule for the Management of Elephants in South Africa*. Pretoria.
- Department of Rural Development and Land Reform. 2013. *Land Audit as approved by Cabinet September 5 2013*. Pretoria.
- Dercon, S. 1998. Wealth, risk and activity choice: cattle in Western Tanzania. *Journal of Development Economics* **55**:1–42.

- Devillers, R., R. L. Pressey, A. Grech, J. N. Kittinger, G. J. Edgar, T. Ward, and R. Watson. 2015. Reinventing residual reserves in the sea: Are we favouring ease of establishment over need for protection? *Aquatic Conservation: Marine and Freshwater Ecosystems* **25**:480–504.
- Di Minin, E., I. Fraser, R. Slotow, and D. C. MacMillan. 2013. Understanding heterogeneous preference of tourists for big game species: implications for conservation and management. *Animal Conservation* **16**:249–258.
- Dietz, T., E. Ostrom, and P. C. Stern. 2003. Struggle to govern the commons. *Science* **302**:1907–1912.
- Donohue, I. et al. 2016. Navigating the complexity of ecological stability. *Ecology Letters* **19**: 1172–1185.
- Eagles, P. F. J. 2009. Governance of recreation and tourism partnerships in parks and protected areas. *Journal of Sustainable Tourism* **17**:231–248.
- Edgar, G. J. et al. 2014. Global conservation outcomes depend on marine protected areas with five key features. *Nature* **506**:216–220.
- Ellis, F. 2000. *Rural Livelihoods and Diversity in Developing Countries*. Oxford University Press, Oxford.
- Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* **1**:488–494.
- Epstein, G., J. M. Vogt, S. K. Mincey, M. Cox, and B. Fischer. 2013. Missing ecology: Integrating ecological perspectives with the social-ecological system framework. *International Journal of the Commons* **7**:432–453.
- Estes, J. A. et al. 2011. Trophic downgrading of planet Earth. *Science* **333**:301–306.
- Fattebert, J., H. S. Robinson, G. Balme, R. Slotow, and L. Hunter. 2015. Structural habitat predicts functional dispersal habitat of a large carnivore: How leopards change spots. *Ecological Applications* **25**:1911–1921.
- Fay, T. H., and J. C. Greef. 2006. Lion, wildebeest and zebra: A predator-prey model. *Ecological Modelling* **196**:237–244.
- Fischer, A. P., and J. C. Bliss. 2008. Behavioral assumptions of conservation policy: Conserving oak habitat on family-forest land in the Willamette Valley, Oregon. *Conservation Biology*

**22**:275–283.

- Fitzsimons, J. A. 2015. Private protected areas in Australia: current status and future directions. *Nature Conservation* **10**:1–23.
- Fitzsimons, J. A., and G. Wescott. 2008. The role of multi-tenure reserve networks in improving reserve design and connectivity. *Landscape and Urban Planning* **85**:163–173.
- Folke, C., S. Carpenter, T. Elmqvist, L. Gunderson, C. S. Holling, and B. Walker. 2002. Resilience and sustainable development: building adaptive capacity in a world of transformations. *Ambio* **31**:437–440.
- Folke, C., S. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* **35**:557–581.
- Folke, C., T. Hahn, P. Olsson, and J. Norberg. 2005. Adaptive Governance of Social-Ecological Systems. *Annual Review of Environment and Resources* **30**:441–473.
- Folke, C., L. Pritchard, F. Berkes, J. Colding, and U. Svedin. 2007. The Problem of Fit between Ecosystems and Institutions: Ten Years Later. *Ecology and Society* **12**:30.
- Foster-Smith, J., and S. M. Evans. 2003. The value of marine ecological data collected by volunteers. *Biological Conservation* **113**:199–213.
- Fox, J., Z. Nie, and J. Byrne. 2012. sem: Structural Equation Models. R package version 3.0-0.
- Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. *Trends in Ecology and Evolution* **28**:86–92.
- Fuller, R. A., K. N. Irvine, P. Devine-Wright, P. H. Warren, and K. J. Gaston. 2007. Psychological benefits of greenspace increase with biodiversity. *Biology letters* **3**:390–394.
- Funston, P. J. 2008. Conservation and management of lions in Southern Africa: Status, threats, utilization and the restoration option. Pages 109–132 in B. M. Croes, R. Buji, H. H. de Iongh, and H. Bauer, editors. *Management and conservation of large carnivores in West and Central Africa*. Institute of Environmental Sciences, Leiden.
- Gabriel, S. C., and C. B. Baker. 1980. Concepts of business and financial risk. *American Journal of Agricultural Economics* **62**:560–564.
- Gallo, J. A., L. Pasquini, B. Reyers, R. M. Cowling, and C. Town. 2009. The role of private conservation areas in biodiversity representation and target achievement within the Little Karoo region, South Africa. *Biological Conservation* **142**:446–454.

- Gallo, T., and L. Pejchar. 2016. Improving habitat for game animals has mixed consequences for biodiversity conservation. *Biological Conservation* **197**:47–52.
- Gallopín, G. C. 2006. Linkages between vulnerability, resilience, and adaptive capacity. *Global Environmental Change* **16**:293–303.
- Geldmann, J., M. Barnes, L. Coad, I. D. Craigie, M. Hockings, and N. D. Burgess. 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biological Conservation* **161**:230–238.
- Gordon, A., L. Bastin, W. T. Langford, A. M. Lechner, and S. A. Bekessy. 2013. Simulating the value of collaboration in multi-actor conservation planning. *Ecological Modelling* **249**:19–25.
- Grossman, D., P. L. Holden, and R. F. H. Collinson. 1999. Veld management on the game ranch. Pages 261–279 in N. Tainton, editor. *Veld management in South Africa*. University of Natal Press, Pietermaritzburg.
- Grove, J. M. 2009. Managing densely settled social-ecological systems. Pages 281–294 in F. S. Chapin, G. P. Kofinas, and C. Folke, editors. *Principles of Ecosystem Stewardship: Resilience-Based Natural Resource Management in a Changing World*. Springer Science & Business Media.
- Guerrero, A., Ö. Bodin, R. R. J. McAllister, and K. A. Wilson. 2015. Achieving social-ecological fit through collaborative governance. *Ecology and Society* **20**:41.
- Guerrero, A. M., R. R. J. McAllister, J. Corcoran, and K. A. Wilson. 2013. Scale mismatches, conservation planning, and the value of social-network analyses. *Conservation Biology* **27**:35–44.
- Gunderson, L. H. 2000. Ecological Resilience--In Theory and Application. *Annual Review of Ecology and Systematics* **31**:425–439.
- Gunderson, L. H., and C. S. Holling. 2002. *Panarchy: understanding transformations in human and natural systems*. Island Press, Washington D.C.
- Gunderson, L. H., S. S. Light, and C. S. Holling. 1995. Lessons from the Everglades: Learning in a turbulent system. *BioScience* **45**:S66–S73.
- Haines-Young, R., and M. Potschin. 2013. *Common International Classification of Ecosystem Services (CICES, Version 4.3)*. Report to the European Environment Agency.
- Hannan, M. T., and J. Freeman. 1977. The population ecology of organizations. *American*

- Journal of Sociology **82**:929–964.
- Hannan, M. T., and J. Freeman. 1984. Structural Inertia and Organizational Change. *American Sociological Review* **49**:149–164.
- Hannan, M. T., and J. H. Freeman. 1986. Where Do Organizational Forms Come From? *Sociological Forum* **1**:50–72.
- Hannan, M. T., L. Pólos, and G. R. Carroll. 2003. Cascading organizational change. *Organization Science* **14**:463–482.
- Hannan, M. T., L. Pòlos, and G. R. Carroll. 2004. The evolution of inertia. *Industrial and Corporate Change* **13**:213–242.
- Hansen, A. J., and R. Defries. 2007. Ecological Mechanisms Linking Protected Areas to Surrounding Lands. *Ecological Applications* **17**:974–988.
- Hardin, G. 1968. The tragedy of the commons. *Science* **162**:1243–1248.
- Hardy, M. J., J. A. Fitzsimons, S. A. Bekessy, and A. Gordon. 2016. Exploring the permanence of conservation covenants. *Conservation Letters*, In press.
- Harrington, R., N. Owen-Smith, P. C. Viljoen, H. C. Biggs, D. R. Mason, and P. Funston. 1999. Establishing the causes of the roan antelope decline in the Kruger National Park, South Africa. *Biological Conservation* **90**:69–78.
- Hausmann, A., R. Slotow, I. Fraser, and E. Di Minin. 2016. Ecotourism marketing alternative to charismatic megafauna can also support biodiversity conservation. *Animal Conservation*, In press.
- Haveman, H. A. 1992. Between a Rock and a Hard Place: Organizational Change and Performance under Conditions of Fundamental Environmental Transformation. *Administrative Science Quarterly* **37**:48–75.
- Hayes, T. M. 2006. Parks, people, and forest protection: an institutional assessment of the effectiveness of protected areas. *World Development* **34**:2064–2075.
- Hayward, M. W. et al. 2007a. The reintroduction of large carnivores to the Eastern Cape, South Africa: an assessment. *Oryx* **41**:205–214.
- Hayward, M. W. et al. 2007b. Practical considerations for the reintroduction of large, terrestrial, mammalian predators based on reintroductions to South Africa's Eastern Cape Province. *The Open Conservation Biology Journal* **1**:1–11.
- Hayward, M. W. 2011. Scarcity in the prey community yields anti-predator benefits. *Acta*



- Oecologia **37**:314–320.
- Hayward, M. W., and G. I. H. Kerley. 2005. Prey preferences of the lion (*Panthera leo*). *Journal of Zoology*, London **267**:309–322.
- Hayward, M. W., J. O’Brien, and G. I. H. Kerley. 2007c. Carrying capacity of large African predators: Predictions and tests. *Biological Conservation* **139**:219–229.
- Heine, K., and H. Rindfleisch. 2013. Organizational decline: A synthesis of insights from organizational ecology, path dependence and the resource-based view. *Journal of Organizational Change Management* **26**:8–28.
- Hilborn, R., T. A. Branch, B. Ernst, A. Magnusson, C. V. Minte-Vera, M. D. Scheuerell, and J. L. Valero. 2003. State of the world’s fisheries. *Annual Review of Earth and Planetary Sciences* **31**:525–554.
- Hilborn, R., J. M. Orensanz, and A. M. Parma. 2005. Institutions, incentives and the future of fisheries. *Philosophical transactions of the Royal Society B: Biological sciences* **360**:47–57.
- Holland, J. 1995. *Hidden Order: How Adaptation Builds Complexity*. Addison-Wesley, Reading.
- Holland, J. 2006. Studying complex adaptive systems. *Journal of Systems Science and Complexity* **19**:1–8.
- Holling, C., and G. Meffe. 1996. Command and control and the pathology of natural resource management. *Conservation Biology* **10**:328–337.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* **4**:1–23.
- Holling, C. S. 1978. *Adaptive environmental assessment and management*. Wiley, London.
- Holling, C. S. 1981. Forest insects, forest fires, and resilience. in H. Mooney, J. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, editors. *Fire Regimes and Ecosystem Properties*. USDA Forest Service General Technical Report WO-26, Washington.
- Holling, C. S. 2001. Understanding the Complexity of Economic, Ecological, and Social Systems. *Ecosystems* **4**:390–405.
- Hunter, L. T. B. 1998. The behavioural ecology of reintroduced lions and cheetahs in the Phinda Resource Reserve, KwaZulu-Natal, South Africa. PhD thesis, University of Pretoria, Pretoria.
- Iacona, G. D., M. Bode, and P. R. Armsworth. 2016. Limitations of outsourcing on-the-ground biodiversity conservation. *Conservation Biology* **30**:1245–1254.

- Iftekhar, M. S., and D. J. Pannell. 2015. "Biases" in Adaptive Natural Resource Management. *Conservation Letters* **8**:388–396.
- Isaacs, J. 2000. The limited potential of ecotourism to contribute to wildlife conservation. *Wildlife Society Bulletin* **28**:61–69.
- Jackson, D. A. 1993. Stopping rules in Principal Components Analysis: A comparison of heuristical and statistical approaches. *Ecology* **74**:2204–2214.
- Janssen, S., and M. K. van Ittersum. 2007. Assessing farm innovations and responses to policies: A review of bio-economic farm models. *Agricultural Systems* **94**:622–636.
- Jenkins, C. N., and L. Joppa. 2009. Expansion of the global terrestrial protected area system. *Biological Conservation* **142**:2166–2174.
- Kabii, T., and P. Horwitz. 2006. A review of landholder motivations and determinants for participation in conservation covenanting programmes. *Environmental Conservation* **33**:11–20.
- Kamal, S., and G. Brown. 2015. Conservation on private land: a review of global strategies with a proposed classification system. *Journal of Environmental Planning and Management* **58**:576–597.
- Kates, R. W., W. C. Clark, R. Corell, J. M. Hall, C. C. Jaeger, I. Lowe, H. J. McCarthy, J.J. Schellnhuber, B. Bolin, N. M. Dickson, and S. Faucheux. 2001. Sustainability science. *Science* **292**:641–642.
- Keith, D. A., T. G. Martin, E. McDonald-Madden, and C. Walters. 2011. Uncertainty and adaptive management for biodiversity conservation. *Biological Conservation* **144**:1175–1178.
- Kenward, R. E. et al. 2011. Identifying governance strategies that effectively support ecosystem services, resource sustainability, and biodiversity. *Proceedings of the National Academy of Sciences of the United States of America* **108**:5308–5312.
- Kerley, G. I. H., B. G. S. Geach, and C. Vial. 2003. Jumbos or bust: do tourists' perceptions lead to an under-appreciation of biodiversity. *South African Journal of Wildlife Research* **33**:13–21.
- Kerley, G. I. H., and M. Landman. 2006. The impacts of elephants on biodiversity in the Eastern Cape subtropical thickets. *South African Journal of Science* **102**:395–402.
- Kettles, R., and R. Slotow. 2009. Management of free-ranging lions on an enclosed game

- reserve. *South African Journal of Wildlife Research* **39**:23–33.
- Koontz, T. M., and J. Bodine. 2008. Implementing ecosystem management in public agencies: Lessons from the U.S. bureau of land management and the forest service. *Conservation Biology* **22**:60–69.
- Krug, W. 2001. Private supply of protected land in southern Africa: A review of markets, approaches, barriers and issues. Pages 1–42 Workshop Paper World Bank / OECD International Workshop on Market Creation for Biodiversity Products and Services Paris, 25 and 26 January 2001.
- Kusmanoff, A. M., M. J. Hardy, F. Fidler, G. Maffey, C. Raymond, M. S. Reed, J. A. Fitzsimons, and S. A. Bekessy. 2016. Framing the private land conservation conversation: Strategic framing of the benefits of conservation participation could increase landholder engagement. *Environmental Science and Policy* **61**:124–128.
- Langholz, J. 1996. Economics, objectives, and success of private nature reserves in sub-Saharan Africa and Latin America. *Conservation Biology* **10**:271–280.
- Langholz, J. A., and W. Krug. 2004. New Forms of Biodiversity Governance: Non-State Actors and the Private Protected Area Action Plan. *Journal of International Wildlife Law & Policy* **7**:9–29.
- Langholz, J. A., J. P. Lassoie, D. Lee, and D. Chapman. 2000. Economic considerations of privately owned parks. *Ecological Economics* **33**:173–183.
- Langholz, J., and J. Lassoie. 2001. Perils and promise of privately owned protected areas. *BioScience* **51**:1079–1085.
- Larkin, P. A. 1977. An epitaph for the concept of maximum sustained yield. *Transactions of the American fisheries society* **106**:1–11.
- Larson, E. R., A. G. Boyer, and P. R. Armsworth. 2014. A lack of response of the financial behaviors of biodiversity conservation nonprofits to changing economic conditions. *Ecology and Evolution* **4**:4429–4443.
- Laundre, J. W., L. Hernandez, and W. J. Ripple. 2010. The Landscape of Fear: Ecological Implications of Being Afraid. *The Open Ecology Journal* **3**:1–7.
- Laurance, W. et al. 2012. Averting biodiversity collapse in tropical forest protected areas. *Nature* **489**:290–294.
- Leverington, F., K. L. Costa, H. Pavese, A. Lisle, and M. Hockings. 2010. A global analysis of

- protected area management effectiveness. *Environmental Management* **46**:685–698.
- Levin, S. A. 1998. Ecosystems and the Biosphere as Complex Adaptive Systems. *Ecosystems* **1**:431–436.
- Levin, S. A. 1999. *Fragile Dominion: Complexity and the Commons*. Perseus Books, Reading.
- Lindkvist, E., and J. Norberg. 2014. Modeling experiential learning: The challenges posed by threshold dynamics for sustainable renewable resource management. *Ecological Economics* **104**:107–118.
- Lindsey, P. A., R. Alexander, M. G. L. Mills, S. Romañach, and R. Woodroffe. 2007. Wildlife viewing preferences of visitors to protected areas in South Africa: Implications for the role of ecotourism in conservation. *Journal of Ecotourism* **6**:19–33.
- Lindsey, P. A., V. R. Nyirenda, J. I. Barnes, M. S. Becker, R. McRobb, C. J. Tambling, W. A. Taylor, F. G. Watson, and M. T'Sas-Rolfes. 2014. Underperformance of African protected area networks and the case for new conservation models: Insights from Zambia. *PLoS ONE* **9**:e94109.
- Lindsey, P. A., S. S. Romañach, and H. T. Davies-Mostert. 2009. The importance of conservancies for enhancing the value of game ranch land for large mammal conservation in southern Africa. *Journal of Zoology, London* **277**:99–105.
- Lindsey, P., C. J. Tambling, R. Brummer, H. Davies-Mostert, M. Hayward, K. Marnewick, and D. Parker. 2011. Minimum prey and area requirements of the Vulnerable cheetah *Acinonyx jubatus*: implications for reintroduction and management of the species in South Africa. *Oryx* **45**:587–599.
- Little, L. R., A. E. Punt, C. M. Dichmont, N. Dowling, D. C. Smith, E. A. Fulton, M. Sporcic, and R. J. Gorton. 2016. Decision trade-offs for cost-constrained fisheries management. *ICES Journal of Marine Science* **73**:494–502.
- Liu, J. et al. 2007. Complexity of coupled human and natural systems. *Science* **317**:1513–1516.
- Loucks, C., J. Springer, S. Palminteri, J. Morrison, and H. Strand. 2004. *From the vision to the ground: a guide to implementing ecoregion conservation in priority areas*. Worldwide Fund for Nature, Washington D.C.
- Ludwig, D., D. D. Jones, and C. S. Holling. 1978. Qualitative analysis of insect outbreak systems; the spruce budworm and forest. *Journal of Animal Ecology* **44**:315–332.
- Maciejewski, K., J. Baum, and G. S. Cumming. 2016. Integration of private land conservation

- areas in a network of statutory protected areas: Implications for sustainability. *Biological Conservation* **200**:200–206.
- Maciejewski, K., and G. S. Cumming. 2015. The relevance of socioeconomic interactions for the resilience of protected area networks. *Ecosphere* **6**:1–14.
- Maciejewski, K., A. De Vos, G. S. Cumming, C. Moore, and D. Biggs. 2015. Cross-scale feedbacks and scale mismatches as influences on cultural services and the resilience of protected areas. *Ecological Applications* **25**:11–23.
- Maciejewski, K., and G. I. H. Kerley. 2014a. Understanding tourists' preference for mammal species in private protected areas: Is there a case for extralimital species for ecotourism? *PloS ONE* **9**:e88192.
- Maciejewski, K., and G. I. H. Kerley. 2014b. Elevated elephant density does not improve ecotourism opportunities: convergence in social and ecological objectives. *Ecological Applications* **24**:920–926.
- Maechler, M., P. Rousseeuw, A. Struyf, M. Hubert, M. Studer, and P. Roudier. 2015. Package “cluster.”
- Magole, L. I., and L. Magole. 2011. Revisiting Botswana's High-Value, Low-Volume Tourism. *Tourism Analysis* **16**:203–210.
- Mayer, A. L., and P. M. Tikka. 2006. Biodiversity conservation incentive programs for privately owned forests. *Environmental Science and Policy* **9**:614–625.
- McAllister, R. R. J., I. J. Gordon, M. A. Janssen, and N. Abel. 2006. Pastoralists' responses to variation of rangeland resources in time and space. *Ecological Applications* **16**:572–583.
- McDonald-Madden, E., P. W. J. Baxter, R. A. Fuller, T. G. Martin, E. T. Game, J. Montambault, and H. P. Possingham. 2010. Monitoring does not always count. *Trends in Ecology and Evolution* **25**:547–550.
- McGehee, N. G. 2014. Volunteer tourism: evolution, issues and futures. *Journal of Sustainable Tourism* **22**:847–854.
- McGinnis, M. D. 2010. Building a Program for Institutional Analysis of Social-Ecological Systems: A Review of Revisions to the SES Framework. Workshop in Political Theory and Policy Analysis, Bloomington.
- McGranahan, D. A. 2011. Identifying ecological sustainability assessment factors for ecotourism and trophy hunting operations on private rangeland in Namibia. *Journal of Sustainable*

- Tourism **19**:115–131.
- Mellahi, K., and A. Wilkinson. 2004. Organizational failure: A critique of recent research and a proposed integrative framework. *International Journal of Management Reviews* **5**:1–40.
- Mendez, P. F., N. Isendahl, J. M. Amezaga, and L. Santamaria. 2012. Facilitating transitional processes in rigid institutional regimes for water management and wetland conservation: Experience from the Guadalquivir Estuary. *Ecology and Society* **17**:26.
- Millenium Ecosystem Assessment. 2005. *Ecosystems and Human Well-being: Synthesis Report*. Island Press, Washington.
- Miller, K. D., and P. Bromiley. 1990. Strategic risk and corporate performance: An analysis of alternative risk measures. *Academy of Management Journal* **33**:756–779.
- Miller, S. M. et al. 2013. Management of reintroduced lions in small, fenced reserves in South Africa: an assessment and guidelines. *South African Journal of Wildlife Research* **43**:138–154.
- Miller, S. M., and P. J. Funston. 2014. Rapid growth rates of lion (*Panthera leo*) populations in small, fenced reserves in South Africa: a management dilemma. *South African Journal of Wildlife Research* **44**:43–55.
- Mir, D. F., and K. Dick. 2012. Conservation Approaches to Protecting Critical Habitats and Species on Private Property. *Natural Areas Journal* **32**:190–198.
- Moon, K., and C. Cocklin. 2011. A Landholder-Based Approach to the Design of Private-Land Conservation Programs. *Conservation Biology* **25**:493–503.
- Moore, C., J. Grewar, and G. S. Cumming. 2015. Quantifying network resilience: comparison before and after a major perturbation shows strengths and limitations of network metrics. *Journal of Applied Ecology* **53**:636–645.
- Mora, C. et al. 2011. Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. *PLoS Biology* **9**:e1000606.
- Mwangi, E. 2006. The footprints of history: path dependence in the transformation of property rights in Kenya's Maasailand. *Journal of Institutional Economics* **2**:157–180.
- Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. Da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. *Nature* **403**:853–858.
- Naidoo, R., A. Balmford, P. J. Ferraro, S. Polasky, T. H. Ricketts, and M. Rouget. 2006. Integrating economic costs into conservation planning. *Trends in Ecology and Evolution*

**21**:681–687.

- Naidoo, R., G. Stuart-Hill, L. C. Weaver, J. Tagg, A. Davis, and A. Davidson. 2011. Effect of diversity of large wildlife species on financial benefits to local communities in northwest Namibia. *Environmental and Resource Economics* **48**:321–335.
- Naughton-Treves, L., J. Alix-Garcia, and C. A. Chapman. 2011. Lessons about parks and poverty from a decade of forest loss and economic growth around Kibale National Park, Uganda. *Proceedings of the National Academy of Sciences of the United States of America* **108**:13919–13924.
- Naughton-Treves, L., M. B. Holland, and K. Brandon. 2005. The Role of Protected Areas in Conserving Biodiversity and Sustaining Local Livelihoods. *Annual Review of Environment and Resources* **30**:219–252.
- Newton, A. 2011. Social-ecological resilience and biodiversity conservation in a 900-year-old protected area. *Ecology and Society* **16**:13.
- Norberg, J., and G. S. Cumming. 2008. Complexity theory for a sustainable future. Columbia University Press, New York.
- Norgaard, R. B. 2008. Finding hope in the millennium ecosystem assessment. *Conservation Biology* **22**:862–869.
- North, D. 1990. Institutions, Institutional Change, and Economic Performance. Cambridge University Press, Cambridge.
- Norton, D. A. 2000. Editorial: Conservation Biology and Private Land: Shifting the Focus. *Society for Conservation Biology* **14**:1221–1223.
- Novelli, M., J. I. Barnes, and M. Humavindu. 2006. The Other Side of the Ecotourism Coin: Consumptive Tourism in Southern Africa. *Journal of Ecotourism* **5**:62–79.
- OECD. 2016. Organisation for economic co-operation and development. Available from (OECD (<http://stats.oecd.org/>)). (accessed May 20, 2016).
- Oksanen, A. J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O. Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2015. Community Ecology Package: Vegan. Version 2.3-0.
- Ostrom, E. 1990. Governing the commons. Cambridge University Press, New York.
- Ostrom, E. 2007. A diagnostic approach for going beyond panaceas. *Proceedings of the National Academy of Sciences of the United States of America* **104**:15181–15187.

- Ostrom, E. 2009a. Understanding institutional diversity. Princeton University Press, Oxfordshire.
- Ostrom, E. 2009b. A general framework for analyzing sustainability of social-ecological systems. *Science* **325**:419–22.
- Ostrom, E. 2010. Polycentric systems for coping with collective action and global environmental change. *Global Environmental Change* **20**:550–557.
- Owen-Smith, N., and M. Mills. 2008. Predator-prey size relationships in an African large-mammal food web. *Journal of Animal Ecology* **77**:173–183.
- Owley, J., and A. R. Rissman. 2016. Trends in private land conservation: Increasing complexity, shifting conservation purposes and allowable private land uses. *Land Use Policy* **51**:76–84.
- Packer, C. et al. 2013. Conserving large carnivores: dollars and fence. *Ecology Letters* **16**:635–641.
- Palomo, I., C. Montes, B. Martin-Lopez, J. A. Gonzalez, M. Garcia-Llorente, P. Alcorlo, and M. R. G. Mora. 2014. Incorporating the Social-Ecological Approach in Protected Areas in the Anthropocene. *BioScience* **64**:181–191.
- Paloniemi, R., and P. M. Tikka. 2008. Ecological and social aspects of biodiversity conservation on private lands. *Environmental Science and Policy* **11**:336–346.
- Paloniemi, R., and V. Vilja. 2009. Changing ecological and cultural states and preferences of nature conservation policy: The case of nature values trade in South-Western Finland. *Journal of Rural Studies* **25**:87–97.
- Pamo, E. T. 1998. Herders and wildlife behaviour as a strategy against desertification in northern Cameroon. *Journal of Arid Environments* **39**:179–190.
- Pasquini, L. 2007. Privately-owned lands and biodiversity conservation: analysing the role of Private Conservation Areas in the Little Karoo, South Africa. PhD thesis, University of Sheffield, Sheffield.
- Pasquini, L., R. M. Cowling, C. Twyman, and J. Wainwright. 2010a. Devising appropriate policies and instruments in support of private conservation areas: lessons learned from the Klein Karoo, South Africa. *Conservation Biology* **24**:470–478.
- Pasquini, L., C. Twyman, and J. Wainwright. 2010b. Toward a conceptual framework for blending social and biophysical attributes in conservation planning: a case-study of privately-conserved lands. *Environmental Management* **46**:659–670.
- Pegas, F. D. V., and J. G. Castley. 2014. Ecotourism as a conservation tool and its adoption by



- private protected areas in Brazil. *Journal of Sustainable Tourism* **22**:604–625.
- Pegas, F. D. V., and J. G. Castley. 2016. Private reserves in Brazil: Distribution patterns, logistical challenges, and conservation contributions. *Journal for Nature Conservation* **29**:14–24.
- Peterson, G. D., S. R. Carpenter, and W. A. Brock. 2003. Uncertainty and the management of multistate ecosystems: an apparent rationale route to collapse. *Ecology* **84**:1403–1411.
- Petraitis, P. S., and C. Hoffman. 2010. Multiple stable states and relationship between thresholds in processes and states. *Marine Ecology Progress Series* **413**:189–200.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* **307**:321–326.
- Poiani, K. A., B. D. Richter, M. G. Anderson, and H. E. Richter. 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. *BioScience* **50**:133–146.
- Polasky, S., S. R. Carpenter, C. Folke, and B. Keeler. 2011. Decision-making under great uncertainty: Environmental management in an era of global change. *Trends in Ecology and Evolution* **26**:398–404.
- Poppenborg, P., and T. Koellner. 2013. Do attitudes toward ecosystem services determine agricultural land use practices? An analysis of farmers' decision-making in a South Korean watershed. *Land Use Policy* **31**:422–429.
- Power, R. J. 2003. Evaluating how many lions a small reserve can sustain. *South African Journal of Wildlife Research* **33**:3–11.
- Pressey, R. L., P. Visconti, and P. J. Ferraro. 2015. Making parks make a difference: poor alignment of policy, planning and management with protected-area impact, and ways forward. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **370**:20140280.
- R Development Core Team, R. 2013. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* **43**:223–225.
- Rissman, A. R., and N. F. Sayre. 2012. Conservation Outcomes and Social Relations: A Comparative Study of Private Ranchland Conservation Easements. *Society & Natural Resources* **25**:523–538.
- Rockström, J. et al. 2009. A safe operating space for humanity. *Nature* **461**:472–475.
- Ropke, I. 2004. The early history of modern ecological economics. *Ecological Economics*

**50**:293–314.

- Ross, S. A., R. Westerfield, and B. D. Jordan. 2008. *Fundamentals of corporate finance*, 12th edition. Tata McGraw-Hill Education, Winsted.
- Rouget, M., D. M. Richardson, and R. M. Cowling. 2003. The current configuration of protected areas in the Cape Floristic Region, South Africa - reservation bias and representation of biodiversity patterns and processes. *Biological Conservation* **112**:129–145.
- Ruef, M. 2000. The Emergence of Organizational Forms: A Community Ecology Approach. *American Journal of Sociology* **106**:658–714.
- Ruseva, T. B., J. R. Farmer, and C. Chancellor. 2016. Networking for conservation: social capital and perceptions of organizational success among land trust boards. *Ecology and Society* **21**:50.
- Schaich, H., C. Bieling, and T. Plieninger. 2010. Linking Ecosystem Services with Cultural Landscape Research. *GAIA - Ecological Perspectives for Science and Society* **19**:269–277.
- Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* **413**:591–596.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: Linking theory to observation. *Trends in Ecology and Evolution* **18**:648–656.
- Scholes, R. J., and R. Biggs. 2004. Ecosystem services in Southern Africa: a regional assessment. *Millennium Ecosystem Assessment*.
- Scott, J. M., F. W. Davis, R. G. McGhie, R. G. Wright, C. Groves, and J. Estes. 2001. Nature reserves: Do they capture the full range of America's biological diversity? *Ecological Applications* **11**:999–1007.
- Selinske, M. J., J. Coetzee, K. Purnell, and A. T. Knight. 2015. Understanding the motivations, satisfaction, and retention of landowners in private land conservation programs. *Conservation Letters* **8**:282–289.
- Seymour, C. L., S. J. Milton, G. S. Joseph, W. R. J. Dean, T. Ditlhobolo, and G. S. Cumming. 2010. Twenty years of rest returns grazing potential, but not palatable plant diversity, to Karoo rangeland, South Africa. *Journal of Applied Ecology* **47**:859–867.
- Sheil, D., and D. F. R. P. Burslem. 2013. Defining and defending Connell's intermediate disturbance hypothesis: A response to Fox. *Trends in Ecology and Evolution* **28**:571–572.
- Shipley, B. 2002. *Cause and correlation in Biology*. Cambridge University Press, Cambridge.

- Sims-Castley, R., G. I. H. Kerley, G. Beverley, and J. Langholz. 2005. Socio-economic significance of ecotourism-based private game reserves in South Africa's Eastern Cape Province. *Parks* **15**:6–18.
- Skinner, J. D., and C. T. Chimimba. 2005. *The Mammals of the Southern African Subregion*. Cambridge University Press, Cambridge.
- Smit, B., and J. Wandel. 2006. Adaptation, adaptive capacity and vulnerability. *Global Environmental Change* **16**:282–292.
- Spear, D., L. C. Foxcroft, H. Bezuidenhout, and M. A. McGeoch. 2013. Human population density explains alien species richness in protected areas. *Biological Conservation* **159**:137–147.
- Spierenburg, M., C. Steenkamp, and H. Wels. 2008. Enclosing the local for the global commons: community land rights in the Great Limpopo Transfrontier Conservation Area. *Conservation and Society* **6**:87–97.
- Squires, D., and N. Vestergaard. 2013. Technical change in fisheries. *Marine Policy* **42**:286–292.
- Starfield, A. M., and A. L. Bleloch. 1986. *Building Models for Conservation and Wildlife Management*. The Burgess Press, Edina, Minnesota.
- Stein, G. 2003. Respect the unstable. *IEEE Control Systems Magazine* **23**:12–25.
- Stieglitz, N., Thorbjørn Knudsen, and M. C. Becker. 2016. Adaptation and inertia in dynamic environments. *Strategic Management Journal* **37**:1854–1864.
- Stirling, A. 2007. A general framework for analysing diversity in science, technology and society. *Journal of the Royal Society, Interface* **4**:707–719.
- Stolton, S., K. H. Redford, and N. Dudley. 2014. *The Futures of Privately Protected Areas*. Gland, Switzerland.
- Strickland-Munro, J. K., H. E. Allison, and S. A. Moore. 2010. Using resilience concepts to investigate the impacts of protected area tourism on communities. *Annals of Tourism Research* **37**:499–519.
- Sukhdev, P. W., H. Schröter-Schlaack, C. Nesshöver, C. Bishop, and J. Brink. 2010. The economics of ecosystems and biodiversity: mainstreaming the economics of nature: a synthesis of the approach, conclusions and recommendations of TEEB (No. 333.95 E19). Ginebra.
- Swift, B., V. Arias, S. Bass, and C. Chacón. 2004. *Private Lands Conservation in Latin America*:

- The Need for Enhanced Legal Tools and Incentives. *Journal of Environmental Law and Litigation* **19**:85–149.
- Sydow, J., G. Schreyog, and J. Koch. 2009. Organizational path dependence: Opening the black box. *Academy of Management Review* **34**:689–709.
- Tambling, C. J., D. J. Druce, M. W. Hayward, J. G. Castley, J. Adendorff, and G. I. H. Kerley. 2012. Spatial and temporal changes in group dynamics and range use enable anti-predator responses in African buffalo. *Ecology* **93**:1297–1304.
- Tambling, C. J., and J. T. du Toit. 2005. Modelling wildebeest population dynamics: implications of predation and harvesting in a closed system. *Journal of Applied Ecology* **42**:431–441.
- Turner, B. L. et al. 2003. A framework for vulnerability analysis in sustainability science. *Proceedings of the National Academy of Sciences of the United States of America* **100**:8074–8079.
- Van den Berg, E. C., C. Plarre, H. M. Van den Berg, and M. W. Thompson. 2008. The South African National Land Cover 2000. Report No. GW/A/2008/86. Pretoria, South Africa.
- Von Hase, A., M. Rouget, and R. M. Cowling. 2010. Evaluating private land conservation in the cape lowlands, South Africa. *Conservation Biology* **24**:1182–1189.
- Walker, B., L. Gunderson, A. Kinzig, C. Folke, S. Carpenter, and L. Schultz. 2006. A handful of heuristics and some propositions for understanding resilience in social-ecological systems. *Ecology and Society* **11**:13.
- Walker, B. H., and M. A. Janssen. 2002. Rangelands, pastoralists and governments: interlinked systems of people and nature. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* **357**:719–25.
- Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**:473–498.
- Walker, B., and C. Holling. 2004. Resilience, adaptability and transformability in social-ecological systems. *Ecology and Society* **9**:5.
- Wallace, G. N., D. M. Theobald, T. Ernst, and K. King. 2008. Assessing the ecological and social benefits of private land conservation in Colorado. *Conservation Biology* **22**:284–296.
- Walters, C. 1986. Adaptive management of renewable resources. MacMillan Publishers, New York.

- Walters, C., and C. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* **71**:2060–2068.
- Ward, J. 1963. Hierarchical grouping to optimize an objective function. *Journal of the American Statistical Association* **58**:236–244.
- Watson, J. E. M., N. Dudley, D. B. Segan, and M. Hockings. 2014. The performance and potential of protected areas. *Nature* **515**:67–73.
- Wearing, S. 2001. *Volunteer tourism: Experiences that make a difference*. Cabi Publishing, New York.
- Williams, B. K. 2015. Integrating external and internal learning in resource management. *The Journal of Wildlife Management* **79**:148–155.
- Williamson, O. E. 1981. The economics of organization: The transaction cost approach. *American Journal of Sociology* **87**:548–577.
- Willock, J., I. J. Deary, G. Edwards-Jones, G. J. Gibson, M. J. McGregor, A. Sutherland, J. B. Dent, O. Morgan, and R. Grieve. 1999a. The Role of Attitudes and Objectives in Farmer Decision Making: Business and Environmentally-Oriented Behaviour in Scotland. *Journal of Agricultural Economics* **50**:286–303.
- Willock, J., I. J. Deary, M. M. McGregor, A. Sutherland, G. Edwards-Jones, O. Morgan, B. Dent, R. Grieve, G. Gibson, and E. Austin. 1999b. Farmers' Attitudes, Objectives, Behaviors, and Personality Traits: The Edinburgh Study of Decision Making on Farms. *Journal of Vocational Behavior* **54**:5–36.
- Wolf, E. 1972. Ownership and political ecology. *Anthropology Quarterly* **45**:201–205.
- World Conservation Union. 2003. *The Durban action plan: Vth IUCN World Parks Congress*, Durban, South Africa. Gland, Switzerland.
- Wright, H. E., and M. L. Heinselman. 1973. The ecological role of fire in natural conifer forests of western and northern America. *Quaternary Research* **3**:317–513.
- Yu, D. J., H. C. Shin, I. Pérez, J. M. Anderies, and M. A. Janssen. 2016. Learning for resilience-based management: Generating hypotheses from a behavioral study. *Global Environmental Change* **37**:69–78.